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LOCOMOTION AND SOME ASSOCIATED MORPHOLOGY  
IN THE NORTHERN FLYING SQUIRREL

by

CYRIL GLADSTONE HAMPSON

A THESIS

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FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled Locomotion and Some Associated Morphology in the Northern Flying Squirrel submitted by Cyril Gladstone Hampson in partial fulfilment of the requirements for the degree of Doctor of Philosophy.



## ABSTRACT

Some aspects of the locomotion and associated morphology of the northern flying squirrel, Glaucomys sabrinus sabrinus were investigated during the years 1960 to 1965 inclusive. A limited amount of study of the southern flying squirrel, Glaucomys volans and of the red squirrel, Tamiasciurus hudsonicus preblei was done for purposes of comparison.

The morphological work involved investigation of growth rates, body and skin densities and areas of various body surfaces, as well as the extent and activation of the cartilaginous rod which partially supports the patagium. The locomotor activities studied involved progression upon horizontal and vertical surfaces, as well as progression through the air. The latter included analyses of trajectory, gliding, parachuting, launching, landing, braking, turning and a minimal investigation of airflow. Much of the work was done by the use of single and multiple-image high speed still photography as well as by slow motion cinematography.

In general, growth rates were not unlike those which have been recorded for other mammals. Birth was followed by a period of rapid growth which tapered off gradually. The young were well furred by the twentieth day. The lower incisors erupted on day 22 while the upper incisors did not appear until day 33. Eyes opened between day 29 and day 33.

Early attempts at locomotion occurred on the first day as the





young squirrels attempted to squirm forward on the belly while moving the limbs in an uncoordinated fashion. By day 4 they were able to turn over when placed on their back and could turn in circles about the pelvis using the front limbs for propulsion. On day 6 the young were able to cling to the fingers when handled and could support the head in an upright position. On day 12 they were observed progressing backward by pushing with the fore limbs and at this time also exhibited the spreading reflex when suspended by the tail. The young were observed ascending vertical surfaces slowly on day 40, but were unable to descend. By day 49 they were able to prop themselves on their haunches, freeing the fore feet for food handling. After much head-bobbing, the young were observed to take horizontal jumps measuring 6-8 inches on day 58. By this time, they were also able to descend tree-trunks. Leaps of 2-3 ft, involving fully spread patagia, were recorded on day 66 while by day 70 they were able to glide for distances up to 6 ft.

The total density of intact northern flying squirrels was found to be significantly lower than that of red squirrels, while densities of the skinned bodies and skins of the two species were not significantly different. The difference in total densities appeared to be caused by the fact that northern flying squirrels have more cutaneous tissue and pelage than red squirrels.

The patagium is partially controlled by a cartilaginous rod





averaging 28.2 mm in length and attached laterally to the pisiform bone. This rod is adducted and abducted by opposing musculature.

Northern flying squirrels were observed walking, when crawling as juveniles, when foraging casually for food upon the ground, and when descending tree-trunks slowly. In the adults, support often alternated between two, three and four feet, while in juveniles the support pattern involved three and four feet successively.

Trotting was observed only when the squirrels were progressing along slender branches and occurred both when the animals were right side up and when they were upside down. Occasionally the trot was briefly transitional between the walk and bound.

Most of the observed progression of northern flying squirrels upon horizontal surfaces was by means of the bound or half-bound. These gaits were characterized by conspicuous arching of the spine associated with the over-reach of the hind limbs. Two periods of suspension were observed, a relatively long one during which the body was stretched out in mid-air, and a much shorter one when the front limbs left the running surface immediately prior to the contact of the hind ones. Recorded rates for G. volans were slightly higher than those for G. sabrinus.

Both species of North American flying squirrels tended to lay scent trails when introduced into new surroundings.

Northern flying squirrels tend to ascend trees by means of a



footfall pattern in which fore and hind limbs move in pairs. When descending they may either walk or use the front and hind feet in paired fashion.

Travel through the air is characterized by gliding and parachuting. Short trajectories are essentially parabolic but the patagia exert a retardatory effect upon the rate of descent. Launching is accomplished by the combined pull of the fore limbs and the powerful thrust of the hind limbs. Braking is associated with manoeuvring the broad ventral surface into a position approximately perpendicular to the line of flight. When landing upon horizontal surfaces, the hind feet commonly make contact before the front feet, while this order is reversed when landing upon vertical surfaces.

Northern flying squirrels can make relatively sharp 90-degree turns, spiral descents, and even negotiate sudden changes of direction through 180 degrees while in the air. Turning appears to be initiated by the lowering of a front limb and the relaxation of the tension on the patagium on the same side, together with flipping the tail in the direction of the turn. Airflow appears to be laminar during gliding phases, but turbulence develops as the squirrel brakes for landing.

Gliding in the mammals appears to have evolved independently on at least three occasions, possibly four. Flying phalangers of the subfamily Phalangerinae (Order Marsupialia) are represented by the genera Petaurus, Acrobates and Schoinobates occurring in Australia,



Tasmania, New Guinea and various islands to the north. The Dermoptera is represented by a single genus, Cynocephalus, of Asia. Two African genera of gliding mammals, Anomalurus and Idiurus, are listed with the ?Sciuromorpha under the subfamilies Anomalurinae and Zenerellinae respectively. An additional twelve genera of gliding mammals are listed under the subfamily Petauristinae of the family Sciuridae. The latter occur in North America, Europe, Asia, Ceylon, and the Indonesian Islands. Study skins and skeletons housed in the British Museum reveal a great range in size and coloration as well as more subtle differences in morphology.

Gliding and parachuting also occur in various species of fish, amphibians and reptiles. A well-developed sense of balance and the ability to control aerial attitude appear to be basic to successful gliding.





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Frontispiece.

Glaucomys sabrinus gliding overhead.

Photograph at 1/5000 sec.







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## I. INTRODUCTION

### Purpose of the Study

The central purpose of this study was to attempt to analyze the major types of locomotor activity characteristic of the northern flying squirrel (Glaucomys sabrinus) and investigate some of the associated morphology. An attempt was made to record representative aspects of this behavior photographically and to quantify the results by means of grids and known exposure rates. A limited amount of data was gathered on the red squirrel, (Tamiasciurus hudsonicus), and the southern flying squirrel, (Glaucomys volans), for purposes of comparison. The aim was to clarify a number of relationships between morphology and function, and possibly point the way for further studies in connection with other gliding and parachuting forms. It is hoped too, that the methods and procedures developed in this study might prove useful to subsequent investigators.

There have been relatively few studies of a serious nature published on the northern flying squirrel and practically nothing, of an analytical nature, has been recorded with respect to its various modes of locomotion. Radvanyi (1959) did a study of inherent activity rhythms of the species in relation to illumination and to lunar and solar photoperiodism. Davis (1963) completed a study of the reproductive ecology of the northern flying squirrel in Saskatchewan. Howell (1918) and Seton (1928) published accounts of the life history of the



species; the former also revised the classification and distribution of North American flying squirrels in the same paper. Cowan (1936) described two litters of Glaucomys sabrinus taken by him in British Columbia, and refers to two other females taken at Indianpoint Lake, British Columbia. In the same paper, Cowan briefly discusses the breeding of this species in British Columbia, the appearance of the young, and nesting habits. Bourlière (1956) devotes about one-half page of his book to a discussion of the gliding of "the North American flying squirrel."

#### Other Locomotion Studies.

Apparently man has long been interested in animal locomotion. From the days of the early cave men in Paleolithic times to the present day, there have been many attempts to depict both man and beast engaged in various representative activities. Judged by the attitudes and proportions of the subjects represented some of the early workers were observant indeed. However, it has only been in the last century that animal locomotion has been extensively studied.

One of the great monumental works in the early scientific study of locomotion was undertaken by Edweard Muybridge, who published most of his results in 1887 under the title "Animal Locomotion." Since Muybridge pioneered the application of photography to the analysis of animal locomotion, his work is cited at some length.

In 1872, while directing the photographic surveys of the United States Government on the Pacific Coast, according to Muybridge





himself (1899), in the city of San Francisco the old controversy was re-opened as to whether a fast trotting horse ever experiences a period of transit, in any part of his stride, during which all four feet are off the ground at the same time. Muybridge set out to solve the problem photographically. The solution was not easy. For the most part, wet collodion plates were slow and every photographer was in a large measure his own chemist, preparing his own dipping baths, making his own collodion, coating and developing his own plates and frequently manufacturing his own chemicals. However, at the Sacramento race track in May, 1872 Muybridge succeeded in securing a number of sufficiently sharp photographs to show that in the rapidly executed trot of a horse periods of suspension do occur when all four feet are off the ground at once.

So the immediate problem was solved. However, each of the photographs made at this time illustrated a more or less different phase of trotting action. Selecting a number of these, Muybridge endeavored to arrange consecutive phases of a complete stride. This, however in consequence of the irregularity of the intervals, he was unable to accomplish satisfactorily. It then occurred to him that what he required was a series of photographic images made in rapid succession regulated at appropriate intervals of time or distance.

Muybridge then secured the cooperation of Mr. Leland Stanford and continued his research at the latter's stockfarm, now the present site of Stanford University. Here, he shortly devised a motor clock





mechanism for making and breaking electric circuits which, in turn, could be made to trigger the shutters of his cameras. The rates could be regulated at discretion. In the year 1878, he deposited in the Library of Congress, Washington, a series of sheets of photographs illustrating several equidistant consecutive phases of one complete stride of a horse while walking, trotting, galloping, etc. entitled, "The Horse in Motion."

Muybridge wished to continue with his work but on a much more comprehensive scale using the newly discovered dry-plate process. However, it was not possible to find publishers willing to take such financial risks. At this time, the University of Pennsylvania, through the influence of its Provost, Dr. William Pepper, instructed Muybridge to carry on the new investigation under its auspices. Hence, he recommenced his outdoor labors in the spring of 1884 and finished in the autumn of 1885. Muybridge states that more than 100,000 photographic plates were used in the preparation of the work for the press.

Muybridge's studio, apparatus and methods of working are interesting. He generally worked outdoors where a shed 37 m long, open at the front and divided vertically and horizontally by threads strung five cm apart, served as the lateral background. The track lay immediately in front of the shed while fixed backdrops were erected at either end of the track. On specific occasions, these backdrops were sometimes supplemented by portable units. In the actual photography, Muybridge made use of three batteries of cameras, a battery of 24



located laterally at intervals and parallel to the track, and a battery of 12 cameras situated at either end so that lateral, front-foreshortening and rear-foreshortening photographs could be taken simultaneously. Synchronization of the shutters in the various batteries of cameras was achieved electrically by running wires from common binding posts to specific cameras in each series. A chronograph was used for recording the intervals of time between successive exposures.

In practice, it was necessary to make trial runs in order to determine the total time required for the phases being recorded. Total time was then divided into appropriate intervals. The motor clock was powered by an adjustable weight attached to a cord wound round a drum, the speed being regulated partially by a fan wheel. Fastened to the frame of the clock was a ring of hard rubber in which were inserted 24 insulated segments of platinum which in turn were connected by insulated wires to 24 binding posts. A rod in the centre, complete with contact brush, rotated making successive contacts with the platinum inserts thus closing circuits and firing the cameras. The chronograph, equipped with style and tuning fork vibrating at 100 vibrations per second, recorded the time intervals. The vibrations were divided into tenths and the intervals calculated in thousandths of a second. Time intervals of exposure varied from  $1/100$  second to several seconds. While  $1/1000$  second was found sufficiently fast for most occasions, very rapid exposures were made at approximately  $1/6000$  second. In addition, Muybridge (1887) notes that in some cases exposures were





made by the subjects thrusting against threads stretched across the track, while on other occasions the wheels of vehicles to which horses were harnessed depressed wires, thus completing electrical circuits.

Finally, using the succession of footfalls as a basis, Muybridge concluded that quadrupeds when progressing upon the ground employ eight different regular systems of progressive motion. These he described as the walk, amble, trot, rack or pace, canter, transverse gallop, lateral gallop and ricochet. Any other patterns observed or recorded were treated as accidental.

Some years later A.B. Howell carried out comprehensive locomotion studies using the slow motion camera and published many of his findings in 1944 under the title "Speed in Animals." Howell's investigations considered the muscular system, skeletal characteristics and body proportions as well as gaits. He found it most logical to divide quadrupedal gaits into three main groups, two of them symmetrical and one, asymmetrical in rhythm. He classified the symmetrical gaits as two-time, in which two feet are placed at the same instant and four-time, in which each foot is placed at a different instant from the rest. The trot and pace were treated as examples of the former while the walk exemplified the latter. Howell (1944) cites the gallop as the common instance of an asymmetrical gait. All of these gaits are characterized by varying patterns, the variations often resulting from different speeds with which they are executed. Howell





considers the bound and half-bound essentially as symmetrical renditions of the asymmetrical gallop. Altogether, Howell recognized the following gaits and their variations: diagonal walk, lateral walk, running walk or single-foot, walking trot, trot, walking pace, pace, transverse gallop, lateral gallop, canter, bound, half-bound, bipedal walk and run, bipedal walk or ricochet.

Bartholomew and Caswell (1951) made use of a high-speed electronic flash unit in order to clarify some of the details of bipedal and quadrupedal locomotion in kangaroo rats. Bourlière, (1956) in his chapter on locomotion, correctly represents four successive stages in the landing of the "North American" flying squirrel upon a vertical tree-trunk. Although Bourlière fails to state whether the illustrations are sketches from observations or reproductions from photographs, I would suspect the latter from the accuracy of limb attitudes depicted.

Of late, Hildebrand has made extensive use of slow motion pictures for the functional analysis of vertebrate locomotion. Hildebrand (1963) feels that too often the parts of the body have been studied independently and that function has been inferred from structure or estimated by casual observation. He notes that morphologists, today, are placing increasing emphasis upon the study of living animals in order to refine and extend interpretations of structure. In 1963, Hildebrand briefly reviewed the work of Muybridge and Howell with respect to the use of footfall formulae in the determination and description of gaits in vertebrates. He draws attention to the fact that



these workers did not take into consideration the importance of the relative durations of the various support patterns characteristic of specific types of locomotion, i.e. two animals, though using the same footfall formula, may in fact be using different gaits because of differences in the relative durations of various support patterns involved.

By studying his films frame by frame in a viewer equipped with a frame counter Hildebrand was able to prepare "gait diagrams" which included both footfall formulae and the duration of each pattern of support represented. He then isolated two important variables characteristic of symmetrical gaits and plotted them, one against the other on a simple grid (Fig. 1). The variable represented on the abscissa was the percentage of stride, in time, that each foot is on the ground. For instance, a slowly moving animal may have each foot on the ground 70 to 90 % of the time while a rapidly moving animal may have each foot on the ground for only 20 to 30 % of the time. On the ordinate was plotted the other variable, the percentage of stride that fore foot follows ipsilateral hind foot, also in time. It is readily apparent that if there is no lag, both feet on the same side of the body move in unison and the animal in question is pacing. Hildebrand (1963) explains further that if the lag is 10 to 15 %, we have a lateral sequence of footfalls in which the footfalls of the lateral feet are more closely spaced than the footfalls of diagonal feet giving us a lateral sequence, lateral couplets gait, 1, 2--3, 4. If the



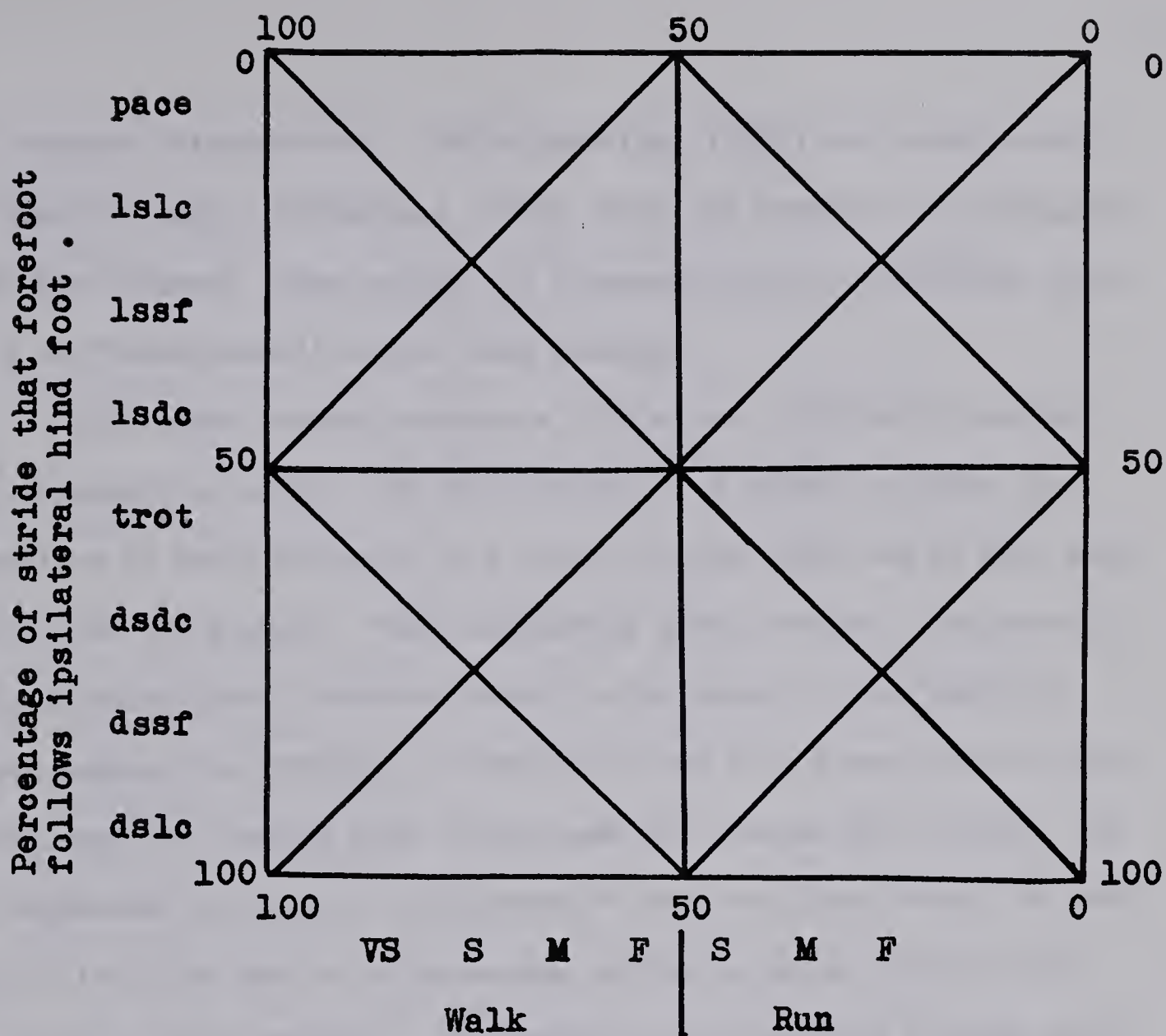


lag is 25 %, the gait is an even four beat one, 1-2-3-4, the lateral sequence, single-foot characteristic of some horses. If the lag is 35 to 40 %, the lateral sequence is still retained but now diagonal footfalls are more closely spaced than laterals and so we have a lateral sequence, diagonal couplets gait 4,1--2,3. When the lag is 50 % diagonal feet move in unison, giving us the trot. And if the lag is more than 50 % the next fore foot to fall after a given hind foot becomes the diagonal one rather than the ipsilateral and we move into the family of diagonal sequence gaits.

Hence, it follows that symmetrical gaits may be expressed by two percentage figures (Hildebrand, 1963). On the abscissa, Hildebrand proposes seven intervals of 10 % each, extending from 20 to 90 %, and terms these: very slow, slow, moderate, and fast walking gaits; slow, moderate, and fast running gaits. On the ordinate, Hildebrand uses eight intervals of  $12\frac{1}{2}$  % termed: pace, lateral sequence lateral couplets gait, lateral sequence single-foot, lateral sequence diagonal couplets gait, trot, and diagonal sequence single-foot. He found no animal using the diagonal sequence lateral couplets gait.

Hildebrand (1963) then draws in the diagonals of his grid, and joins the midpoints of both adjacent and opposite sides forming 16 triangles (Fig. 1). He then finds that all plots falling within one triangle represent gaits having the same footfall formula and that each triangle has a different formula. He found, also, that there is another and different formula at every intersection of lines and along every





Percentage of stride that each foot is on the ground.

lsle - lateral sequence lateral couplets

lssf - lateral sequence single foot

lsdc - lateral sequence diagonal couplets

dsdc - diagonal sequence diagonal couplets

dssf - diagonal sequence single foot

dsle - diagonal sequence lateral couplets

VS - very slow

M- moderate

S - slow

F- fast

FIG. 1. Graph of symmetrical gaits (after Hildebrand).





line between intersections. While Muybridge (1899) had noted several "accidental" gaits, Hildebrand (1963) finds the formulae of such gaits along the diagonal lines and at the intersections; he classifies such gaits as "transitional" rather than abnormal.

Hildebrand appears to have a little more difficulty dealing with asymmetrical gaits. On the abscissa of a graph, he plots the proportion of total duration of a stride during which one or both hind feet are on the ground. Then considering both front and hind pair of feet, he establishes "midtime" which is the point in time which is midway between the striking of the first foot of a given pair and the moment when the leading foot of the same pair leaves the surface. He now expresses the lag of the midtime of the fore feet behind the midtime of the hind feet as a percentage of the duration of stride and plots this on the ordinate. Presumably, this gives him a graph somewhat like that used in the analysis of symmetrical gaits. Hildebrand states that such treatment "permits the interpretation of gait selection in relation to body size, conformation, maneuverability, ancestry, etc."

#### Gliding Vertebrates and Their Distribution

While this study is concerned with the northern flying squirrel, Glaucomys sabrinus sabrinus, a gliding squirrel native to North America, there are many other contemporary gliders as well as a number of extinct forms in the three orders Marsupialia, Dermoptera and Rodentia. Simpson (1945) lists three genera in the Order Marsupialia, subfamily



## Phalangerinae:

Petaurus Pleist. - Recent; Australia, Recent; New Guinea.

Flying "opossums", gliders.

Acrobates Recent; Australia. Pygmy flying "opossums",

feather-tails, pygmy gliders.

Schoinobates Recent; Australia. Gliders, flying phalangers,

great flying phalangers.

In the Order Dermoptera Simpson (1945) lists two extinct genera from North America and one living genus from Asia.

Planetetherium U. Paleoc.

Plagiomene L. Eocene.

Cynocephalus Recent; Asia. Colugo, caguan, kubuk, "flying lemur".

But most gliding mammals as listed by Simpson (1945) are rodents in the subfamily Petauristinae under 12 genera, as follows:

Petaurista Pleist. - Recent; Asia. Taguan.

Eupetaurus Recent; Asia (Kashmir). Woolly flying squirrel.

Sciuropterus Recent; Europe, Asia. (Old World) flying squirrel.

Glaucomys Pleist. - Recent; North America. (American) flying squirrel.

Eoglaucomys Recent; Asia. Himalayan flying squirrel.

Hylopetes Recent; S Asia.

Aeretes Recent; Asia (China).

Trogopterus Recent; Asia.

Belomys Recent; Asia.

Pteromyscus Recent; Asia.





Petaurillus Recent; SE Asia.

Iomys Recent; SE Asia.

In addition, Simpson (1945) lists two remaining genera of gliding mammals with the ?Sciuromorpha under the subfamilies Anomalurinae and Zenerellinae, respectively:

Anomalurus Recent; Africa. Scaly-tailed "squirrels".

Idiurus Recent; Africa.

From a study of skins and skeletons of gliding mammals in the British Museum, it is clear that these groups have evolved and radiated widely. The gliding marsupials vary in size from that of a small mouse to species the size of a large domestic cat. All have long tails, often prehensile, though in some species the tails are feather-shaped and plumed, presumably for use as rudders. Sanderson (1955) states that members of the subfamily Phalangerinae are found all over the continent of Australia and in Tasmania, New Guinea, and the islands to the north, even to the Celebes, Timor and Amboina.

The tiny pygmy flying "opossums" of the genus Acrobates are scarcely more than 6 in. in total length and have a narrow, furred patagium stretching from wrist to ankle on either side of the body. The outer margins of the patagia bear longer, light-colored hairs, while the tail is distinctly feather-like (Plates 2 and 4). They tend to be brownish above and creamy-white below, while the slender digits bear large terminal pads and long claws for climbing. Members of this group of marsupials are reminiscent of the gliding "mice" of





the genus Idiurus of the subfamily Zenerellinae which are indigenous to the continent of Africa.

Flying phalangers of the genus Petaurus vary in size from less than a foot in length to approximately 2.5 ft. Petaurus breviceps, the small "sugar glider" (Plate 2), is characterized by soft, silky pelage, large eyes and ears, long bushy tail and digits equipped with well-developed claws. They are blue-grey above with a dark, mid-dorsal stripe extending from the tip of the nose to the base of the tail. The dorsal patagia are edged with black while the ventral surfaces tend to be white. Dark and light facial markings are pronounced and complex. Petaurus australis (Plate 2) is a much larger form characterized by warm tan tones dorsally. Extremities of the limbs and tail are dark brown while the ventral surfaces are buffy.

The genus Schoinobates contains the largest of the gliding marsupials, measuring over 3 ft in length. It is found throughout the hilly and mountainous area all down the eastern side of Australia from Queensland to Victoria and more especially in the open gum (eucalyptus) forests (Sanderson, 1955). Their long fluffy pelage varies, individually, from black through various browns and greys to white. Patagia extend from the elbows to the leading edges of the ankles, but lack the supporting cartilaginous rod characteristic of the Petauristinae and Anomalurinae. Sanderson states that they are completely arboreal, and only able to travel on the ground with great clumsiness. Their diet consists of tender leaves, shoots and blossoms



of various eucalyptus and other trees of the Myrtle family.

In the Dermoptera, the patagia appear to be more extensively developed and specialized than in any other patagiate group with the exception of the Chiroptera. The patagium is divided on each side into three well-developed main areas: the propatagium, between the neck and fore limb; the plagiopatagium, between the fore and hind limbs; and the uropatagium, between the hind limb and tail (Plate 3). To these, may be added the interdigital patagia associated with the digits of both front and hind feet. The propatagium rises at the base of the lower jaw, its free margin running thence to the base of the claw of the pollex. Since both the neck and forearm are relatively long, the propatagium is laterally and antero-posteriorly extensive. The free edge of the plagiopatagium runs from the base of the claw of the fifth digit of the fore foot to a corresponding point on the first digit of the hind foot. The free edge of the uropatagium extends from the postaxial side of the fifth digit of the hind foot close to the base of the claw to the tip of the tail forming a true interfemoral membrane as in bats. Attachment of the patagia appears to be such that elbow, knee and heel are relatively free with respect to movement.

Pocock (1926) clarifies a number of specializations with respect to the limbs and tail which support the patagia in the Dermoptera. The distal end of the tail is always so strongly flexed that it may be doubted if it can ever be straightened, much less bent





upward in flight. Both the fore and hind limbs are also greatly restricted in extension. The lower half of the hind leg is tied to the thigh by muscles in such a way that the knee, in extension, can form only a right-angle. The fore limb is not restrained quite to the same extent, but a muscle passing from the edge of the scapula to the fore leg above the elbow and strengthening the patagium in the axilla, prevents the humeral segment of the limb from being extended at right-angles to the spinal axis, and a similar muscle, passing from the distal end of the humerus to proximal end of the radius and occupying the concavity of the elbow, prevents that joint from being straightened so that the lower half of the limb can be in a line with the upper. Both fore and hind feet are fully webbed by means of the interdigital patagia which are of special morphological interest on account of their possible significance in connection with the high development attained by somewhat similar patagia in the fore limb of the Chiroptera.

Members of the Dermoptera are unique in other respects as well. The fore limbs are much longer than the hind ones and the neck appears relatively long for an arboreal form. Sanderson (1955) states that members of this group are basically Insectivora but that their brains have two curious folds not so far observed in any other mammal. The living representatives of the group have four incisors in each jaw as well as canines in the lower jaw. The lower incisors are directed forward and their crowns are comb-like in structure while the outermost





of these teeth, together with the canines, are double-rooted and hence unlike those of all other mammals. The ulna and fibula are inclined backward to some extent, the orbits are surrounded by bone and the placenta is discoidal. Pocock (1926) hypothesized that dermopterans are probably living representatives of the ancestral patagiate form from which the Chiroptera were evolved.

The Anomalurinae and Zenerellinae of Africa appear to occupy ecological niches somewhat similar to those occupied by the Phalangerinae of Australia, the Dermoptera of Asia and the Petauristinae of Asia, Europe and North America. In Idiurus of the subfamily Zenerellinae, the patagium stretches from wrist to ankle, leaving fore and hind feet free and the relatively ill-developed uropatagium is attached to the thigh rather than the tail. The ventral surface of the base of the tail is equipped with small scales behind which are ranged two rows of bristles extending to the tip of the tail. Long vibrissae project from the tail, increasing the total surface area. Members of this genus are arboreal and communal, living in the tops of large hollow trees (Sanderson, 1955). They are approximately the size of a large deermouse (Peromyscus) (Plate 4).

The Anomalurinae are represented by a single genus, Anomalurus (Plate 5). In this group, the patagium is partially supported by a long cartilaginous rod attached to the broad flattened olecranon process in the region of the elbow (Plate 6). The patagium extends from the sides of the neck to the wrists, thence to the tip of the



cartilaginous rod, then to the first toe of the hind limb, and finally from the fifth toe to a point about a quarter of the way down the tail. Pocock (1926) notes that next to the Dermoptera, the anomalurids have the most highly developed patagia of all gliding mammals. On the underside of the tail, at its base there is a double line of tough triangular scales with sharp points directed backward (Plate 7). The scales probably assist the animals in climbing and are responsible for their common name, "scale-tails." These interesting mammals have 16 pairs of ribs rather than the usual 12. Part of the masseter passes through the infraorbital canal, while the lateral masseter is restricted to the zygomatic arch, differing in these respects from other rodents except the Dipodoidea and Hystricoidea (Hill, 1961). Anomalurids occur in a bewildering variety of colors and range all over Africa from Gambia to Kenya and south to Nyasaland (Sanderson, 1955). One of the largest forms, Anomalurus pelii from W Africa, is a magnificent animal, jet black above and pearl grey below with vivid white margins edging the patagia (Plate 5). While this species exceeds 2 ft in length, several other species are much smaller.

The subfamily Petauristinae is represented by a vast assemblage of flying squirrels which vary greatly in size and coloration. Among the smallest are the diminutive southern flying squirrel, Glaucomys sabrinus, of North America, and the pygmy flying squirrel, Hylopetes spadiceus, of SE Asia. These forms average approximately 9 in. in total length and weigh in the neighborhood of 4 oz (Palmer, 1954 and





Ellerman, 1961). On the other hand, the giant flying squirrel, Petaurista petaurista, and the red-and-white flying squirrel, Petaurista alborufus, both of Asia, may measure over a yard in length and weigh up to 5 lb (Ellerman, 1961). All have the patagia attached to wrist and ankle and partially supported by a cartilaginous rod projecting from the wrist. All tend to have soft, thick, silky to woolly pelage; short, rather rounded heads; large eyes; and tails which are either bushy or somewhat flattened by the lateral outgrowth of long, plume-like hairs. They are found throughout most of the forested areas of North America, Europe south of Scandinavia and Britain, and throughout Asia south to the Himalayas, India, Ceylon and the Indo-Chinese area, and the Indonesian islands. Most of them are Asiatic, but one (Sciuropterus) is found in Europe and another (Glaucomys) in North America (Sanderson, 1955). The genera are separated on the bases of cranial measurements, dental characters, bullae conformation and external characters.

The British museum has an impressive collection of skins of the Petauristinae, several of which are represented in Plates 8 to 13. However, black and white photographs fail to convey the great beauty and variety of their pelage. Many are strikingly colored. For instance, in Petaurista alborufus (Plate 8) the upper patagia, shoulders, neck and head to the base of the forehead are deep red. The forehead is snow-white, while a large area of gold extends mid-dorsally. Limbs are dark reddish-brown and the long bushy tail is





red with a pronounced black tip.

Petaurista elegans sybilla has a grizzled ochraceous tawny dorsal surface more olivaceous anteriorly, deeply tawny posteriorly. The dorsal patagia are brilliant rufous, while the undersurface is bright ochraceous buff, which contrasts sharply with the rich rufous margins. The head is rather more tawny than the back, and a narrow black line passes forward from eye to muzzle. Ochraceous rufous patches are present in the postauricular region. The entire tail, except for a few black terminal hairs, as well as the extremities of the limbs are a rich tawny rufous.

Petaurista lylei is silver-grizzled above and bright copper ventrally, with limbs, tail and muzzle clove-brown. Other forms range from the light silver-grey of Sciropterus russicus (Plate 9) through the ashy greys of Eupetaurus cinereus (Plate 10) and Petaurista petaurista cineraceus and the grizzled browns of Petaurista leucogenys (Plate 11) and Trogopterus mordax (Plate 12) to the red-browns of Iomys davisoni and Petinomys genibarbis (Plate 13) and the grizzled black of Hylopetes alboniger (Plate 13) and Eoglaucomys fimbriatus (Plate 9).

But gliding and parachuting are not confined to the mammals. Savile (1962) reports that in the flying fishes (Exocoetus) we find what Gray (1953) calls velocity gliding; they depend on the kinetic energy of their moving bodies. Glides of 50 yd are not uncommon and this distance may be greatly exceeded in turbulent conditions. It has been estimated that such glides require a take-off speed of 30 to



35 mph, a speed almost incredible for normal swimming, but photographs show that the tail continues to drive the fish forward after the body breaks out of the water.

Oliver (1951) notes that gliding lizards of the genus Draco of the tropical forests of southeast Asia and the East Indies have a well-developed patagium that is supported by the last six or seven pairs of ribs and capable of being folded like a fan. Draco volans is a skilled glider that can steer well enough to land on a selected tree and is highly manoeuvrable in the air (Savile, 1962). In order to avoid confusion, Oliver divides this general type of descent into two modes, parachuting and gliding, on the basis of the angle that the descent path takes from the vertical line. Thus parachuting can be considered as the making of a retarded descent along a path that deviates from the vertical by not more than 45 degrees, whereas gliding is the performing of a retarded descent along a path of more than 45 degrees from the vertical. Oliver states, further, that it is obvious that these two modes of descent will merge from one to the other as do nearly all modes of locomotion in vertebrates.

Having thus defined these terms, Oliver points out that several other groups such as the leaftailed geckos of Madagascar (Uroplates), and of Australia (Phyllurus) and the fringed geckos of the genus Ptychozoon have all evolved the capacity and habit of parachuting. In the same paper, Oliver (1951) reports a previously unreported parachuting lizard (Anolis carolinensis carolinensis) and







the results of his experiments with this species and the fence lizard (Sceloporus undulatus). The former spread-eagled when dropped and came down in a controlled glide while the latter fell heavily, straight down, with constant thrashing. The only other recent reptiles that have been reported to exhibit such adaptations are the tree snakes of the genera Chrysopelea and Dendrelaphis. The former includes the "flying" snakes in which the mode of descent is parachuting according to the definition of Oliver. The tree snakes check their descent by pulling in the abdomen and flattening the body (Savile, 1962).

Cott (1926) performed a series of interesting experiments with a tree-frog (Hyla venulosa) which ranges from Mexico to Paraguay. Cott had a number of these small frogs released from the top of a tower not less than 140 ft high and situated in an open space where the ground was hard and covered only by a scanty growth of grass. On being released, the frogs leaped into the air, spread their limbs and sailed slowly down, landing at a point 90 ft from the base of the tower, quite uninjured. In the gliding position, the fingers and toes were spread. The experimental animals never failed to assume a constant gliding attitude and always landed right side up. Cott made similar experiments with Rana temporaria. Though this species is about the same size as H. venulosa and has the advantage of a much greater area of web on the feet it fell vertically and heavily, turning over and over in the air. It was purely a matter of chance whether it reached the ground on its feet or on its back. Similar experiments with the



European tree-frog (H. arborea) revealed that this species failed to assume a constant gliding attitude and fell heavily, following a vertical path.

Cott notes that several species of Rhacophorus inhabiting Borneo, Java, Sumatra and Southern India are reported to glide much after the manner of H. venulosa. The evidence he cites is admittedly scanty and some careful experiments would seem to be in order. It is interesting to note that all of the gliding or parachuting forms are reported to assume an aerial attitude, with limbs fully spread, similar to that most characteristic of Glaucornis sabrinus (see Frontispiece) and of Petinomys genibarbis malaccanus, the latter photographed during flight by Liat (1965).

PLATE 2

Gliding marsupials (Phalangerinae) and Glaucmys.

From top to bottom:

Petaurus australis (New South Wales, Australia)

Petaurus breviceps papuanus (female, New Guinea)

Petaurus breviceps papuanus (male, New Guinea)

Acrobates pygmaeus (New South Wales, Australia)

Glaucmys sabrinus (Manitoba, Canada)

Glaucmys volans (W Virginia, U.S.A.)

Photograph of study skins in the British Museum, July,  
1965.

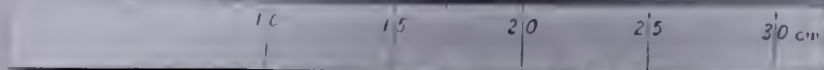




PLATE 3

Cynocephalus (Dermoptera) and Glaucomys.

From left to right:

Cynocephalus variegatus (Java)

Glaucomys volans (W Virginia, U.S.A.)

Note propatagia, plagiopatagia, interdigital patagia and the interfemoral patagium involving the tail in Cynocephalus. Also note the relatively long fore limbs in this gliding form.

Photograph of study skins in the British Museum, July, 1965.

5  
10  
15  
20  
25  
30 cm.

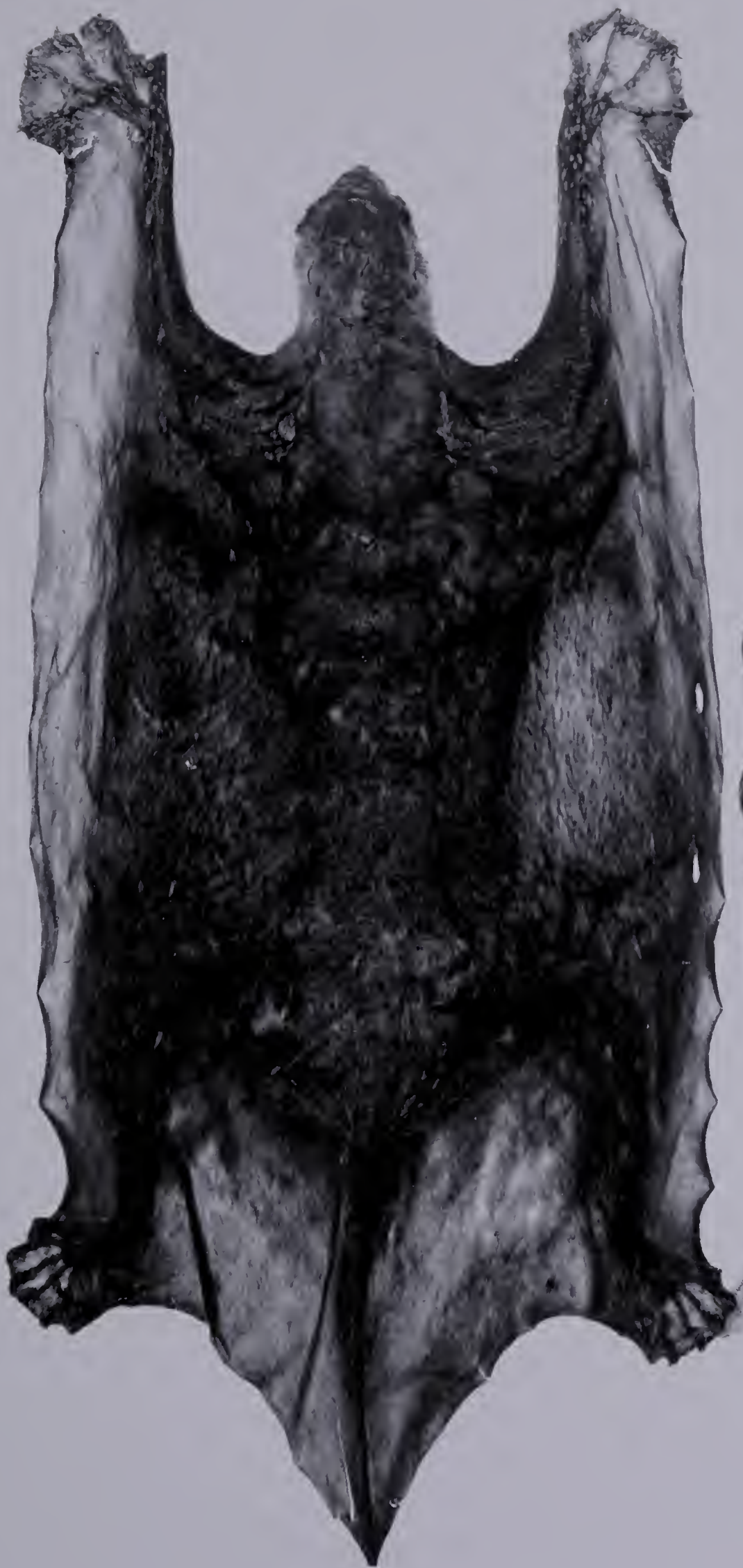


PLATE 4

Acrobates, Idiurus and Glaucmys.

From top to bottom:

Glaucmys volans (W Virginia, U.S.A.)

Idiurus kivuensis (Cameroons, W Africa)

Acrobates pygmaeus (New South Wales, Australia)

Note the relatively small patagia in A. pygmaeus and the supporting cartilaginous rod from the elbow in I. kivuensis.

This plate suggests convergent evolution in the Petauristinae, Anomaluridae and Phalangerinae.

Photograph of study skins in the British Museum, July, 1965.

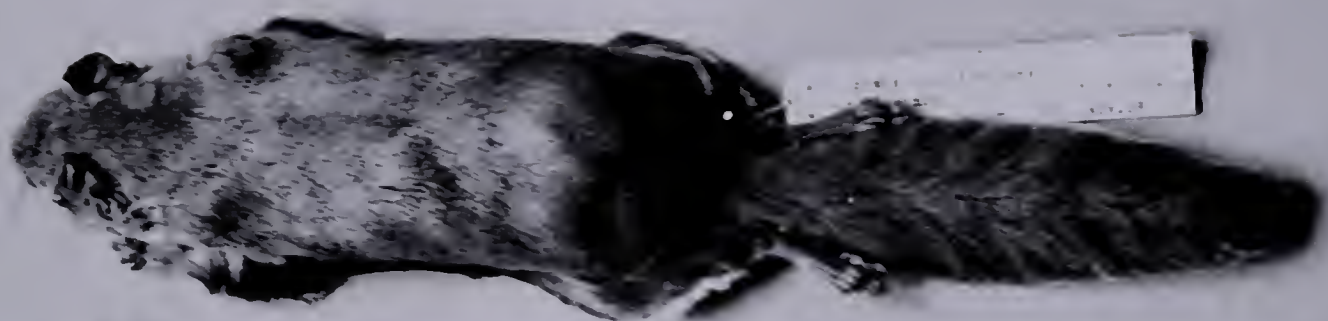


PLATE 5

Anomalurinae and Glaucmys.

From top to bottom:

Anomalurus pelii (Ashanti, W Africa)

Anomalurus jacksoni ( Ituri River, W Africa)

Glaucmys sabrinus (Manitoba, Canada)

Photograph of study skins in the British Museum, July,  
1965.





PLATE 6

Supporting cartilaginous rod, Anomaluridae.

The cartilaginous rod which partially supports the patagium in the Anomaluridae is attached at its base to the olecranon process, rather than to the pisiform bone as in the Petauristinae.

Photograph of study skin of Anomalurus beecrofti in British Museum, July, 1965.

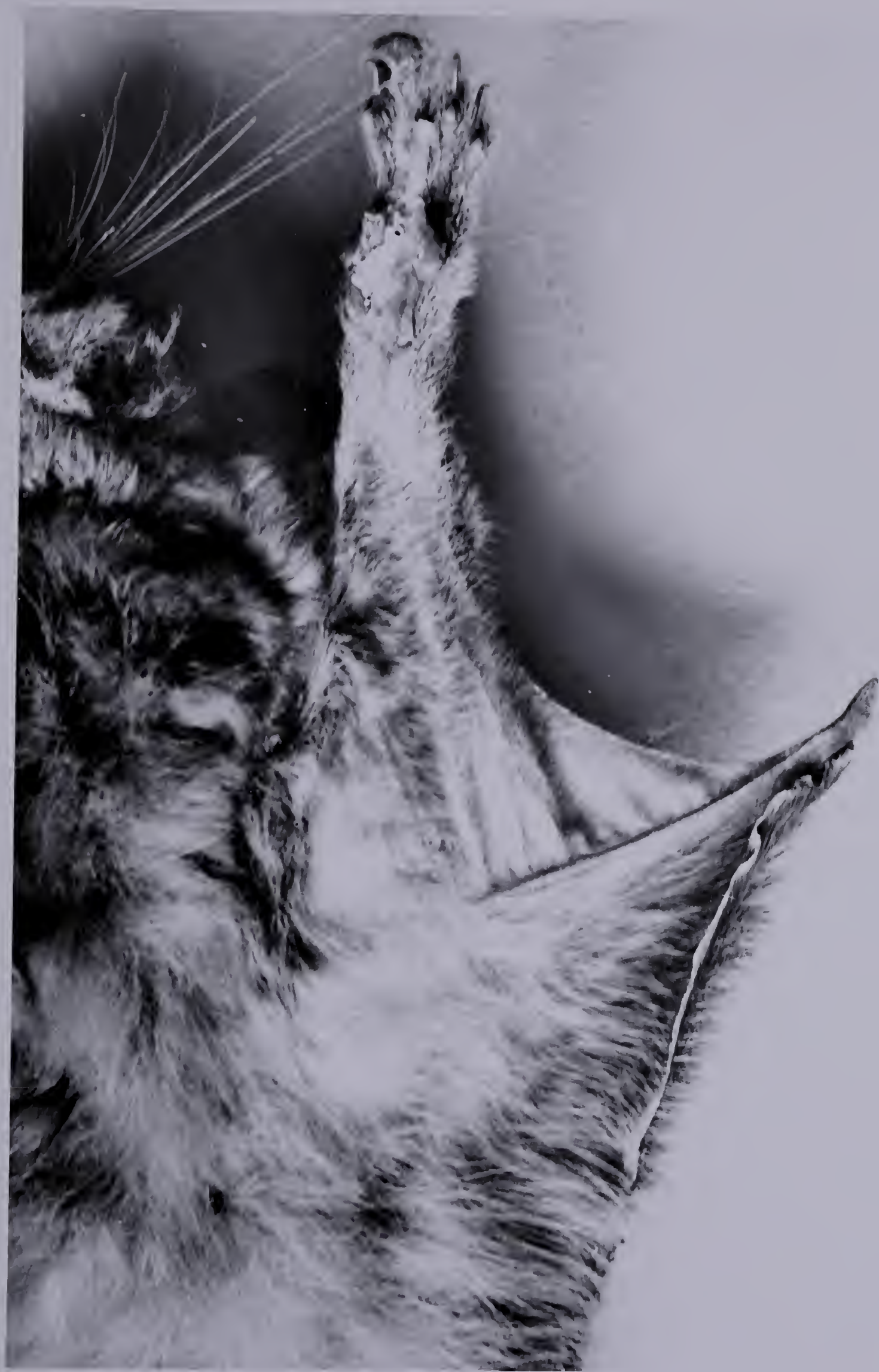


PLATE 7

Scales at the base of tail, Anomaluridae.

The ventral surface of the base of the tail in the Anomaluridae is equipped with a series of imbricated scales with their tips pointing backward. The scales are probably used by these forms in climbing trees.

Photograph of study skin of Anomalurus pelii in British Museum, July, 1965.







PLATE 8

Petaurista and Glaucmys.

From left to right:

Petaurista alborufus (N. Szechwan, China)

Glaucmys sabrinus (Manitoba, Canada)

Petaurista alborufus is one of the largest species of the Petauristinae and is widely distributed throughout SE Asia. This species tends to be deep red in general coloration with white face and varying amounts of grizzling, dorsally.

Photograph of study skins in British Museum, July, 1965.

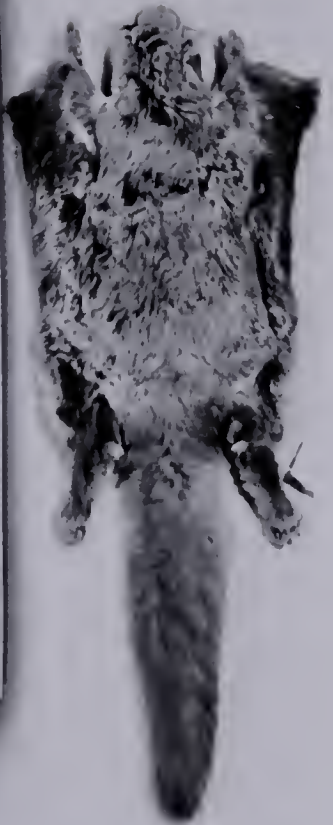
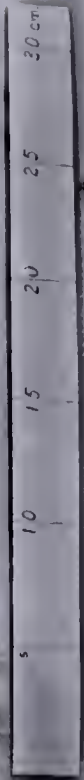


PLATE 9

Eoglaucomys, Aeromys, Sciuropterus and Glaucomys.

From top to bottom:

Eoglaucomys fimbriatus (Kashmir)

Aeromys tephromelas (Malaya)

Sciuropterus russicus (Baltic)

Glaucomys sabrinus (Manitoba, Canada)

Note similarities between Sciuropterus russicus  
and Glaucomys sabrinus.

Photograph of study skins of Petauristinae in British  
Museum, July, 1965.

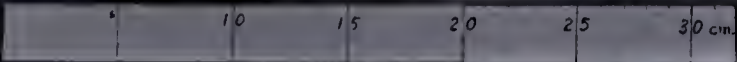
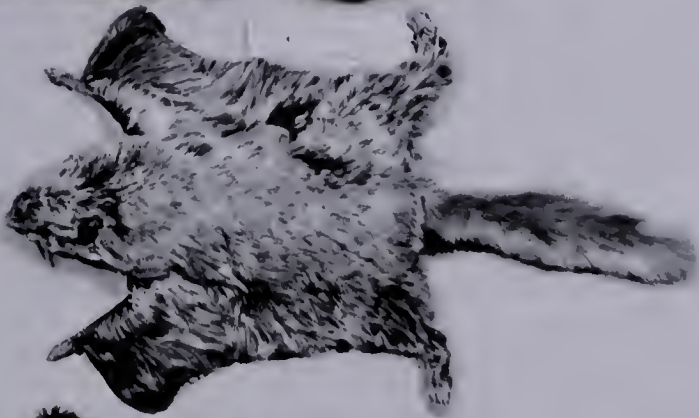




PLATE 10

Eupetaurus and Glaucomys.

From left to right:

Eupetaurus cinereus (Chitral, India)

Glaucomys sabrinus (Manitoba, Canada)

Eupetaurus cinereus is often referred to as the woolly flying squirrel. This is a very large flying squirrel with long dense pelage dorsally and on the tail. It is reported to sometimes inhabit barren cliffs and steep hills.

Photograph of study skins of the Petauristinae in the British Museum, July, 1965.





PLATE 11

Petaurista leucogenys.

This large dark form from Japan has  
very long silky pelage.

Photograph of a study skin of the Petauristinae in the  
British Museum, July, 1965.



PLATE 12

Trogopterus, Belomys, Pteromyscus and Glaucmys.

From top to bottom:

Trogopterus mordax (Ishang, China)

Belomys trichetis (Lower Chindwin, Burma)

Pteromyscus pulverulentus (Kuala Lumpur)

Glaucmys sabrinus (Manitoba, Canada)

Photograph of study skins of the Petauristinae in the  
British Museum July, 1965.



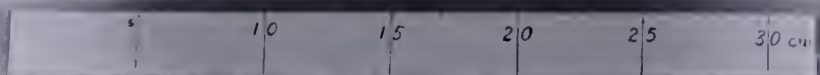




PLATE 13

Petinomys, Hylopetes, Iomys and Glaucomys.

From top to bottom:

Petinomys layardi (Ceylon)

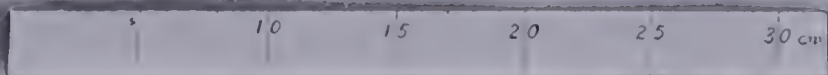
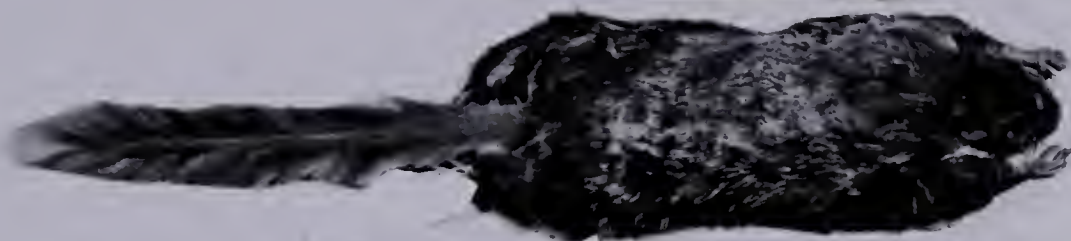
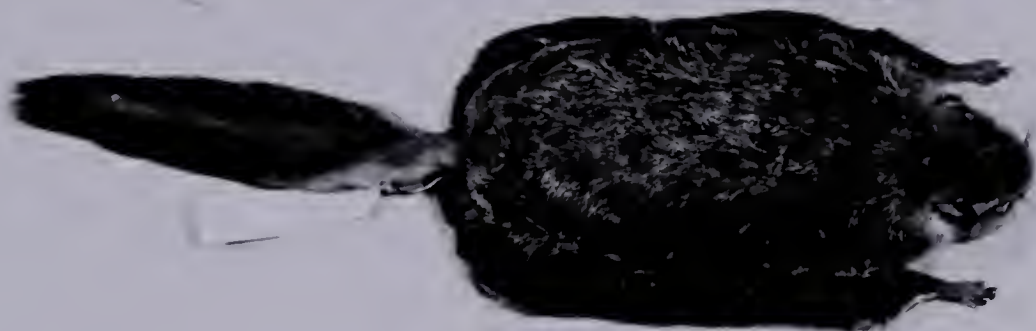
Hylopetes alboniger (Darjeeling)

Iomys davisoni (Penang)

Petinomys genibarbis (Borneo)

Glaucomys sabrinus (Manitoba, Canada)

Photograph of study skins of the Petauristinae in the  
British Museum, July, 1965.





## II. METHODS

### A. Morphological Investigations

#### Density Determinations

The body densities of 20 specimens of Glaucomys sabrinus sabrinus and 14 specimens of Tamiasciurus hudsonicus preblei were investigated for purposes of comparison. The latter were live-trapped in the vicinity of Edmonton, Alberta, during the months of December and January, 1964-65, while live specimens of G. sabrinus were utilized from the experimental population, with the exception of two live-trapped wild animals. The specimens were killed by placing them in a sealed container with a wad of cotton saturated with ether. They were then measured to the nearest millimeter and weighed in air to the nearest 0.1 gram using a triple-beam balance. The nasal orifices and mouth were then plugged with non-absorbent cotton, weights were attached, and the animals were weighed immersed in water (at 68°F) in order to determine total body volume. Before the weights were taken, the specimens were gently agitated in the water for a period of 5 min so that most of the air trapped superficially in the pelage might escape. From these figures gross densities were determined.

Next the specimens were skinned and the densities of the carcasses determined in like manner. Results were then compared statistically and graphed.





### Surface area of Patagia

A number of high speed photographs of individuals in full flight were taken from close range and from directly below the subjects in order to determine characteristic gliding attitude (Frontispiece). It is obvious that the patagia substantially increase the surface area presented to the air when the species is gliding. In order to estimate this increase 11 specimens were killed with ether. The freshly killed specimens were then laid out on 10 x 10 to the inch Dietzgen graph paper and a tracing made around the body, including the tail. The animal was then pinned securely in place and the patagia spread with reference to the gliding attitude determined earlier. A second tracing, superimposed upon the first, was then made. It was now a simple matter of counting squares to arrive at approximations of the surface areas in question.

### Surface Area of Tail

The surface area of the tail was computed in the same manner as the surface area of the patagia.

### Supporting Cartilaginous Rod

The outer margin of the patagium in the region of the wrist is partially supported by a slender cartilaginous rod which is attached, proximally, to a carpal. Several of these rods were removed from the left fore limbs of a number of freshly killed specimens and after measurement were preserved in 10% formalin. Measurements were taken shortly after removal, and they were later photographed against



a dark backdrop (Plate 29). The function of these rods was clarified by means of high speed photographs of the animals gliding overhead, using a black ceiling for backdrop. All such photographs were taken at 1/5000 sec by means of a Dormitzer Synctron electronic flash unit. The activation of the cartilaginous rod was determined by dissection under a ten-power microscope.

#### B. Photographic Studio, Equipment and Techniques

A large photography room measuring 16 ft by 12 ft by 8 ft high was constructed in the basement. One entire end wall, half the ceiling, and many of the climbing, launching, running and landing surfaces were given a light-absorbing matte finish by applying two coats of black Solarite showcard paint. One side wall measuring 16 ft by 8 ft was painted with dull green G.P. 7765 blackboard paint and then graduated in square inches using an Eagle Verithin #734 white blueprint pencil.

The subjects were introduced to the basement room several weeks in advance of the photographic work in order that they might accustom themselves to the new surroundings and move about freely. On no occasion were the animals artificially induced to respond; rather, photographs were taken only after waiting for them to respond of their own volition. It was found necessary to block out extraneous light by sealing the windows and door in order to avoid exposing the film while the shutter of the camera was open, awaiting specific activity on the part of the squirrels.





Equipment included a Hasselblad 500 C,  $2\frac{1}{4} \times 2\frac{1}{4}$  camera with Syncro Compur shutter, Carl Zeiss Planar f 1:2.8, 80 mm lens, single-lens reflex housing and accessory magazine. This camera was used for the majority of the standard speed still shots as well as for the high speed and multiple exposure shots. A Rolleicord  $2\frac{1}{4} \times 2\frac{1}{4}$  camera with Schneider-Kreuznach Xenar f 1:3.5, 75 mm lens was used for a few specific photographs, while in a limited number of other cases an Exakta VX 35 mm camera with a Tessar f 1:3.5 lens was used with Kodachrome 2, daylight color film. In the latter case, the color transparencies were converted to black-and-white with Omega enlarger and Ilford F.P. 3 film. Two motion picture cameras were used, a converted Bell and Howell operating at 128 frames per sec with one-inch lens, and a Cine Special (Kodak) 16 mm f 1:1.9 one-inch lens, running at 64 frames per sec. All film used in the  $2\frac{1}{4} \times 2\frac{1}{4}$  cameras was Ilford F.P. 3 with an A.S.A. rating of 125, while the film used in the motion picture cameras was Kodak Double X negative, A.S.A. (tungsten) 200.

The Ilford film was developed in Ansco Hyfinol for a period of 6 min at 68° F when illumination had been provided by the Dormitzer Syncron, but developing time was increased to 8 min when using the cycling stroboscope as the source of light. Prints were developed in Dektol, one part stock solution to two parts water, for  $1\frac{1}{2}$  min at 68°F. Edwal Quik-Fix was used throughout for fixing both prints and film; instructions supplied by the manufacturer were followed. The printing paper used was single weight Kodabromide F.3 and F.4,





depending upon the contrast of the negative.

Illumination for the motion pictures was supplied by two standard 500 watt floodlights, together with a 650 watt Smith Victor lamp coupled to the camera.

Lighting for all single exposure shots was provided by a high speed Dormitzer Syncron electronic flash unit with accessory lamp. For multiple-exposure still photographs a Type 1532-D Strobolume, triggered by a Type 1531-A Strobotac electronic stroboscope, was used. Both of these instruments were supplied by General Radio Company. The Strobolume was found to provide adequate light while the Strobotac adjusted the intervals between flashes.

Specifications of the Strobolume were as follows:

<u>Flashing Speed Range</u>	continuous, high intensity: 60 per min maximum; intermittent or for short periods: up to 1200 per min; continuous, low-intensity: up to approximately 3000 per min.
<u>Peak light</u>	10 million beam candlepower at 60 flashes per min; 140,000 beam candlepower at 3000 flashes per min.
<u>Flash duration</u>	Approximately 30 microseconds at high intensity; approximately 10 microseconds at low intensity.
<u>Guide number</u>	Approximately 25 at high intensity with film speed of 100 A.S.A.
<u>Power input</u>	105 to 125 volts, 50 to 60 cycles.



Power consumption

At high intensity, 105 watts at 60 frames per min; 500 watts at 1200 frames per min; At low intensity, 120 watts at 3000 frames per min.

Practically all the photographic work was completed before obtaining a photo-electric unit for triggering the lamp when the subject cut the light beam. Up to this point, it was necessary to open the camera shutter manually with one hand while tripping the stroboscope switch synchronously with the other; this was a matter of trial and error.

In the case of single-exposure running shots, the running surface was placed immediately in front of the grid in order to minimize error. Both camera and lamp were placed at a distance of 4 ft from the path of the subject and parallel to the plane of the grid. Thus a large, accurate image was assured on the negative. Camera settings of 1/125 sec at f.22 gave adequate depth of field.

In recording aerial activity, flashing rates of either 600 or 1200 per min were used depending upon the type of locomotion under investigation. Here, light absorption by dull dark surfaces was particularly important so as not to expose the negative either before or after registering the subject. Light for observing the animals and manipulating the equipment was provided by a 15 watt light bulb placed at a distance of 10 ft behind the camera and shielded with a heavy muslin shade. Series of images were secured by opening the shutter for





0.25 sec when the stroboscope was firing at 1200 flashes per min or for 0.5 sec when the unit was firing at 600 flashes per min.

Since one could not expect the experimental animals to perform their characteristic aerial activities immediately in front of a grid, other procedures were used. The cameras were set up at varying distances from the plane of expected activity and pre-focused, the distances dependent upon the nature of the activity under investigation. The black wall 6 ft behind the activity area served as a backdrop. After each series of such photographs was taken, shots were taken of the grid from the same distance. The latter were deliberately underexposed in order to produce a thin negative of the grid. When printing, a negative of the grid, together with one of the activity under study, were both placed in the negative carrier of the enlarger at the same time and printed. Thus the animal was superimposed upon the grid and no corrections for parallax were required.

Airflow was examined briefly by securing four-inch threads of embroidery cotton to the dorsal surface of the squirrel and then photographing the animal gliding in for a landing.

Representative study skins of all genera of gliding mammals of the Phalangerinae, Anomaluridae, Dermoptera and Petauristinae with the exception of Schoinobates were photographed in the British Museum.

A good deal of further information was gathered by observing red squirrels and northern flying squirrels in their natural habitats.



This procedure, however, proved to have definite limitations since their actions tend to occur with such rapidity that finer details cannot be registered with the naked eye.



### III. THE STUDY POPULATION

#### History and Nomenclature

Howell (1918) ably summarizes the history and nomenclature of the North American flying squirrels. He notes that Glaucomys volans early attracted the attention of colonists in the South Atlantic States and that Captain John Smith made specific reference to it in his History of Virginia published in 1624. Ray (1693), Catesby (1743) and Edwards (1751) described this small eastern form rather fully, and the species of southern Mexico was described by Hernandez (1651).

Regarding generic names, Howell (1918) has this to say: "Placed first by Linnaeus in the genus Mus, the American flying squirrels were later associated with Sciurus by Gmelin, Pallas, and Shaw. In 1800 Cuvier proposed a new genus, Pteromys, to include the European flying squirrel (Sciurus volans Linnaeus) and the large East Indian species (Sciurus petaurista Gmelin). The American forms were referred by later writers to this genus. F. Cuvier, in 1823, pointed out the characters distinguishing the American and European flying squirrels from the large Asiatic species, and in 1825 proposed the name Sciuropterus for the European animal, but the name was not generally accepted until Allen adopted it for the American species in his monograph of the Sciuridae (1877). This name continued in current use until 1914, when Miller showed that according to modern rules for fixing types it must give place to Pteromys of earlier date,





the type of the latter having been fixed by Fleming in 1822, on Sciurus volans - the European flying squirrel. Thomas (1908), in a revision of the genera of flying squirrels, separated the American forms subgenerically from the European members of the genus under the name Glaucmys, and in 1915 the present writer raised the group to the generic rank."

Specific names underwent a great many changes from Mus volans of Linnaeus, in the 10th edition of his *Systema Naturae* to the 26 forms recognized in 1915 (see Howell, 1918). However, relationships were far from clear and in 1918 Howell undertook to revise the entire group. Accordingly, he assembled all of the material available, delving into the specimens in the American Museum of Natural History, as well as those in other museums and private collections.

On the basis of the 1052 specimens studied, Howell (1918) proposed two species, volans and sabrinus, for the genus Glaucmys (Plate 14). Howell's volans (1918) consisted of five subspecies: volans (Linnaeus), saturatus Howell, querceti (Bangs), texensis Howell, and goldmani (Nelson); while sabrinus included 19 subspecies: sabrinus (Shaw), makkovikensis (Sornborger), macrotis (Mearns), canescens Howell, bangsi (Rhoads), alpinus (Richardson), yukonensis (Osgood), zaphaeus (Osgood), oregonensis (Bachman), columbiensis Howell, fuliginosus (Rhoads), latipes Howell, olympicus (Elliott), bullatus Howell, klamathensis (Merriman), flaviventris Howell, lascivus (Bangs), californicus (Rhoads), and stephensi (Merriam).



According to Miller and Kellog (1955) volans has been extended since 1918 to include the subspecies madrensis Goldman (1936), underwoodi Goodwin (1936) and herreranus Goldman (1936); while the species sabrinus has been expanded to include griseifrons Howell (1934), lucifugus Hall (1934), fuscus Miller (1936), reductus Cowan (1937), goodwini Anderson (1943) and gouldi Anderson (1943). G. sabrinus latipes was regarded as identical to fuliginosus by Anderson (1946). G. sabrinus coloratus Handley was added in 1953 (Hall and Kelson, 1959).

#### Present Range

Miller and Kellog (1955) outline the known distribution of Glaucomys sabrinus. The species occurs in wooded areas of North America north to the coastal region of Labrador in the east, to James Bay, Hudson Bay, Great Slave Lake and Great Bear Lake more centrally, and to areas inside the Arctic Circle in the Mackenzie basin, Yukon and Alaska; west to east central Alaska, Prince of Wales Island, the western coasts of British Columbia, Washington, Oregon and central California, and the San Bernardino Mountains in southern California; east to Labrador, the eastern coastal regions of Quebec, New Brunswick, Nova Scotia (including Cape Breton Island), Maine, New Hampshire, New York, Vermont, northern Massachusetts, and northern Pennsylvania. The species occurs down the Appalachians to the northeastern regions of West Virginia and northeastern Tennessee. More centrally the range extends as far south as Michigan, Wisconsin, Minnesota, North Dakota and South Dakota. In addition, one tongue extends southwards from







Canada into Montana, Wyoming, Idaho and Utah, while a second tongue extends southwards in California, inland to the San Bernardino Mountains. (Fig. 2)

#### The Experimental Population

The initial experimental specimens of G. sabrinus were live-trapped in the vicinity of Edmonton, Alberta, and housed outdoors in cages located on the eastern margin of a dense, 26-acre bush consisting mostly of white spruce (Picea glauca), balsam poplar (Populus balsamifera), aspen poplar (Populus tremuloides), white birch (Betula papyrifera), willow (Salix spp.) and red-osier dogwood (Cornus stolonifera). They were thus sheltered a good deal from the prevailing winds. Three of the cages measured 4 ft by 8 ft by 6 ft high, while the fourth measured 8 ft by 8 ft by 6 ft high. All cages, including the floors, were covered with one-half-inch galvanized wire mesh. Roofs were constructed of painted plywood and sloped slightly for drainage. Numerous nesting boxes, fashioned from boards or tree-trunks containing woodpecker cavities, were provided. Here, the animals bred and reared their litters.

The experimental population consisted of 123 specimens of Glaucomys sabrinus and 9 specimens of Glaucomys volans, 3 pairs of the latter having been obtained from the University of Michigan, Ann Arbor. According to Howell (1918) and Soper (1964), the subspecies of G. sabrinus was probably sabrinus (Shaw) although this subspecies is known to intergrade with G. sabrinus alpinus (Richardson), the



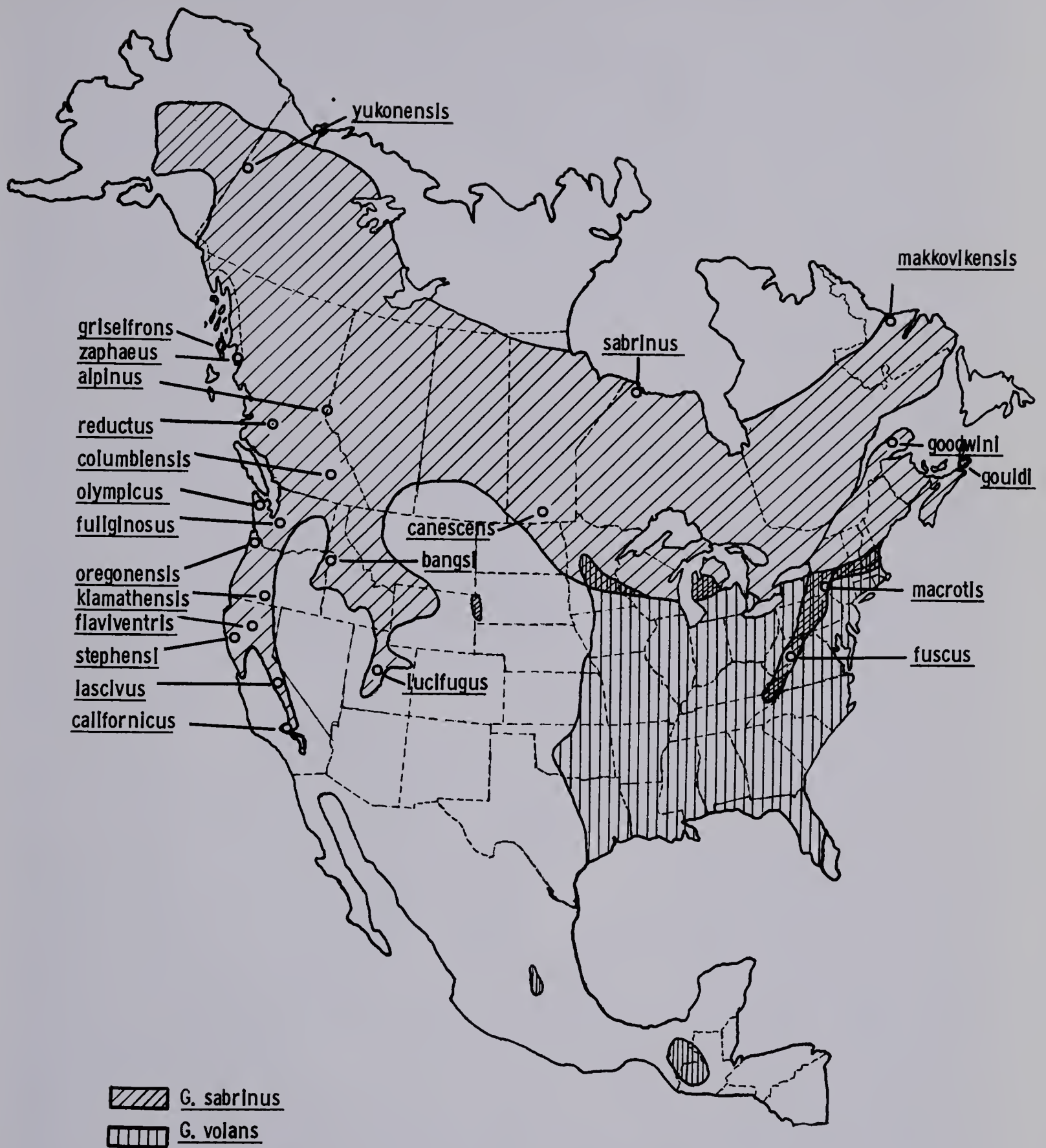


FIG. 2 Range of *Glaucomys sabrinus* and *Glaucomys volans*.

(Type localities for subspecies of *G. sabrinus* are indicated.)  
 (With assistance from Seton, 1928 and  
 Miller and Kellogg, 1955).

PLATE 14

G. sabrinus and G. volans.

Adult female of G. volans on the left  
and adult female of G. sabrinus  
sabrinus on the right.









Rocky Mountain flying squirrel, to the west. The only other flying squirrel occurring in Alberta is G. sabrinus fuliginosus (Rhoads), the dusky flying squirrel, which appears to be confined to the Rocky Mountains of the southwest from Waterton Lakes Park north to about Crowsnest Pass (Soper, 1964). The subspecies of G. volans is doubtful.

Two individuals of G. volans mated in captivity and produced a litter of 3 which were reared without difficulty. Fourteen specimens of G. sabrinus were live-trapped in the vicinity of Edmonton, Alberta. These mated rather freely in captivity and produced a total of 109 young in 29 litters. Eighty-eight young from these litters were reared successfully while 21 died within a few days of birth. The 29 litters of G. sabrinus consisted of five litters of 5 each, thirteen of 4, ten of 3, and a single litter of 2. The mean litter size was 3.75 individuals per litter. Davis (1963) reported three captive females giving birth to 3 young each. Cowan (1936) reported three litters of this species consisting of 3, 3 and 2 young respectively. Svihla (1930) made reference to a female G. volans which gave birth to a litter of 4. Seton (1928) stated that litter size in G. sabrinus varies from 3 to 6. Nevertheless, this study recorded a single litter of 2 and no litters greater than 5.

Three second litters were born during the period of study. In the first case, a female gave birth to a litter of 4 on April 26, 1962 but all died during a cold wet spell which commenced on the day of birth.



The nest had been rather poorly constructed on bare boards and little protection was afforded the young. On July 21, 1962 this female was discovered with a second litter of 3, perhaps a week old. On May 15, 1964 a female gave birth to a litter of 5 which was followed by a second litter of 4 just prior to August 10, 1964. Another female produced a litter of 2 on May 30 of the same year (1964) and a second litter of 4 on approximately July 25. The two females in 1964 raised both litters successfully. Seton (1928) stated that these "industrious little creatures are said to produce three broods in a season" but fails to cite any supporting evidence. On the other hand, Cowan (1936) contends that there is no evidence of more than a single litter per year in this species in Alberta and British Columbia. The three instances of double litters mentioned above are the only ones encountered by the writer in 40 years of rather extensive field work and it is felt that these occurrences might well have been associated with laboratory conditions. The earliest litter date was April 14, and the latest, July 25.

Of 20 litters for which data are complete, the sex ratio was 46:35 in favor of females. While trapping wild specimens of G. sabrinus in Saskatchewan, Davis (1963) secured a ratio of 81 males to 69 females. Neither of these ratios is significantly different from a 1:1 ratio. The difference between Davis's data and mine could be due to a variety of reasons such as differences in mortality rates in the sexes, and the possibility that males might be more readily lured





to baits than females. Also, much of Davis's trapping was done during spring and early summer when the females probably tend to remain closer to the nesting sites with their young.

Another part of the study population consisted of a number of wild specimens which were observed under natural conditions in the field. One wild individual developed the habit of coming rather regularly to a bird-feeding station situated in the proximity of a brilliant yard light, and was observed on numerous occasions during the winter of 1964-65.

For comparative purposes, a total of 16 specimens of the red squirrel, Tamiasciurus hudsonicus preblei, were live-trapped within a 60-mile radius of Edmonton, Alberta.



#### IV. GROWTH RATES

The mean growth rates of one litter of 3 northern flying squirrels, born May 8, 1959 were determined. The data gathered are set down in Appendix A. Figures 3 to 8 illustrate the same material in graph form. Weights were kept from day 2 to day 261. Total length, tail length, hind foot length and ear length were measured from day 2 to day 93, while measurements of cartilaginous rod length were taken from day 1 to day 93, at which time all these measurements approximated the respective figures for adult flying squirrels. The information regarding general development of the young represents a compilation of observations of 6 litters.

##### Weight

While the young flying squirrels increased in weight from a mean of 6.9 g on day 2 to a mean of 156.0 g on day 261, the increase was not constant nor were declines absent (Fig. 3). While gains were relatively slow from day 2 to day 7, the increments registered represent high ratios when compared with the original weight. Increases were rapid and quite steady from day 8 until the young were about 7 weeks old. Weights increased a little more slowly from day 50 to day 93 and still more slowly from day 93 to day 142. A decrease in weight occurred from day 142 to day 156, followed by a more gradual increase to day 198. A rather sharp increase occurred from day 198 to day 220. This increase in mean weight was followed by a slight decrease from day 220 to day 240 and a gradual increase from day 240 to



day 261. The graph, therefore, represents a series of more or less well defined stages of weight gain together with two relatively short periods during which the animals lost weight. The general trend is still upward at day 261 and, although not shown on this graph, the species tends to show a gradual increase in body weight at least until the end of the first year.

The reduced rate of gain after day 50 seems related to the fact that the young are weaned at about 7 weeks. The sharp rise from day 198 to day 220 is probably related to fat deposition for the winter, while the following decline from day 220 to day 240 undoubtedly reflects the fact that December tends to be the month of minimal activity for this species. At this time of the year, they sleep a good deal of the time and ingest relatively little food. I am at a loss to explain the decline from September 26 to October 10.

#### Total Length

The young flying squirrels increased in total length from a mean of 74.1 mm on day 2 to a mean of 301.5 mm on day 93 (Fig. 4). Gains were relatively slow for the first 7 days of this period but increases were rapid and fairly steady thereafter to day 60. Day 60 to day 78 represents two fairly well defined successive periods of reduced gain, while the period from day 78 to day 93 exhibits a marked levelling off trend. By day 93, the young have attained total lengths very close to those characteristic of adult northern flying squirrels.





### Tail Length

The tail increased in length from a mean of 24.0 mm on day 2 to a mean of 144.7 mm on day 93 (Fig. 5). Growth was rapid and relatively steady to day 50, at which time the rate increased very sharply for a period of 6 days. Levelling off occurred in stages after day 56 with the young exhibiting tails of almost maximum length well before day 80. The graphs of total length and tail length are remarkably similar, the increase in tail length being responsible for almost exactly half the increase in total length by day 50. However, tail growth between days 50 to 56 is responsible for 17 of the 25 mm recorded for increase in total length. The tail is very well developed by the time it is required for gliding.

### Hind Foot Length

The length of the hind foot increased from 6.0 mm on day 2 to 41.7 mm on day 83 (Fig. 6). Growth of the hind foot was very rapid from day 2 to day 46 after which the rate tapered off. Near-maximum length was attained on day 69.

### Ear Length

The ear increased in length from a mean of 4.0 mm on day 2 to a mean of 24.0 mm on day 93 (Fig. 7). The short, sharp increase from day 5 to day 6 represents the unfolding of the pinna and its assumption of an upright attitude. Thereafter, to day 26 the length of the ear increased rather slowly. The most rapid growth occurred in the period from day 26 to day 49 by the end of which time the ear had attained



all but about one-sixth of its maximum length. The period from day 49 to day 79 was characterized by rapid tapering off.

#### Cartilaginous Rod Length

The length of the cartilaginous rod attached to the pisiform bone in the wrist increased from a mean of 5.0 mm on day 1 to a mean of 26.1 mm on day 93 (Fig. 8). Growth was very rapid to day 27, after which time increases tapered off. Although near-maximum length had been reached by day 93, the cartilaginous rods of six squirrels, aged 4-5 months, gave a mean of 27.3 mm, while in twenty-one adult squirrels, all over a year in age, the mean rod length was 28.5 mm. In the adult squirrels, the cartilaginous rod varied in length from 25.0 mm to 30.0 mm.

#### General growth and development of the young

The following information is based upon the observation of six litters of northern flying squirrels born on May 8, 1959, May 1, 1960, June 3, 1962, April 14, 1965, April 16, 1965 and April 21, 1965. Litter sizes were 3, 3, 3, 4, 4 and 5 respectively. Early information is often difficult to procure since females which are disturbed at this stage tend to kill and eat their offspring. In 1960 and 1961 five entire litters were lost in this way.

Day 1, (Plates 15 and 16). The skin is pale, pink, translucent, loose and unpigmented with many wrinkles and folds. The patagia are present as loose folds of skin extending from wrist to ankle and from wrist to the sides of the neck.





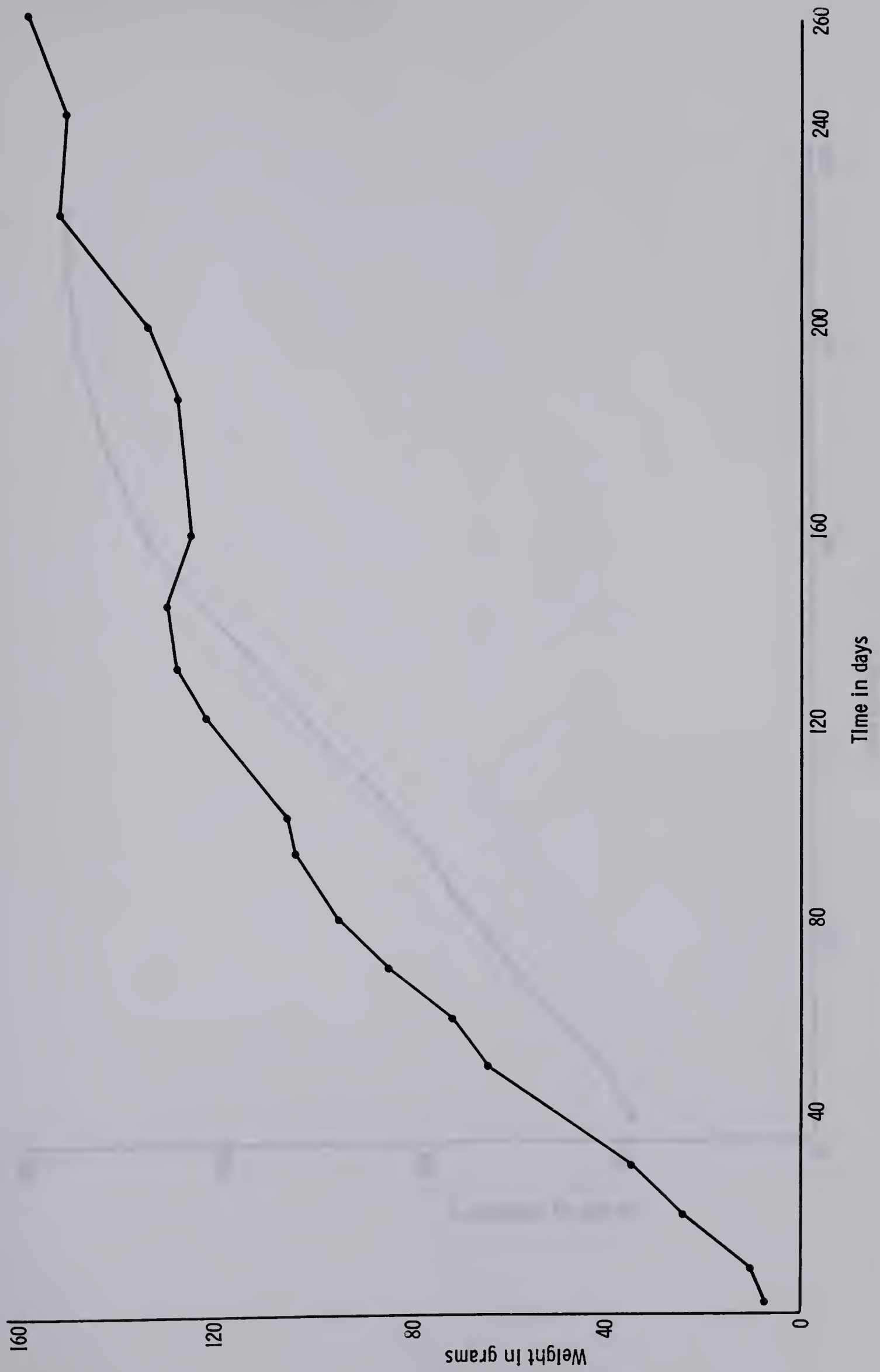


FIG. 3 Mean body weight from day 2 to day 260.



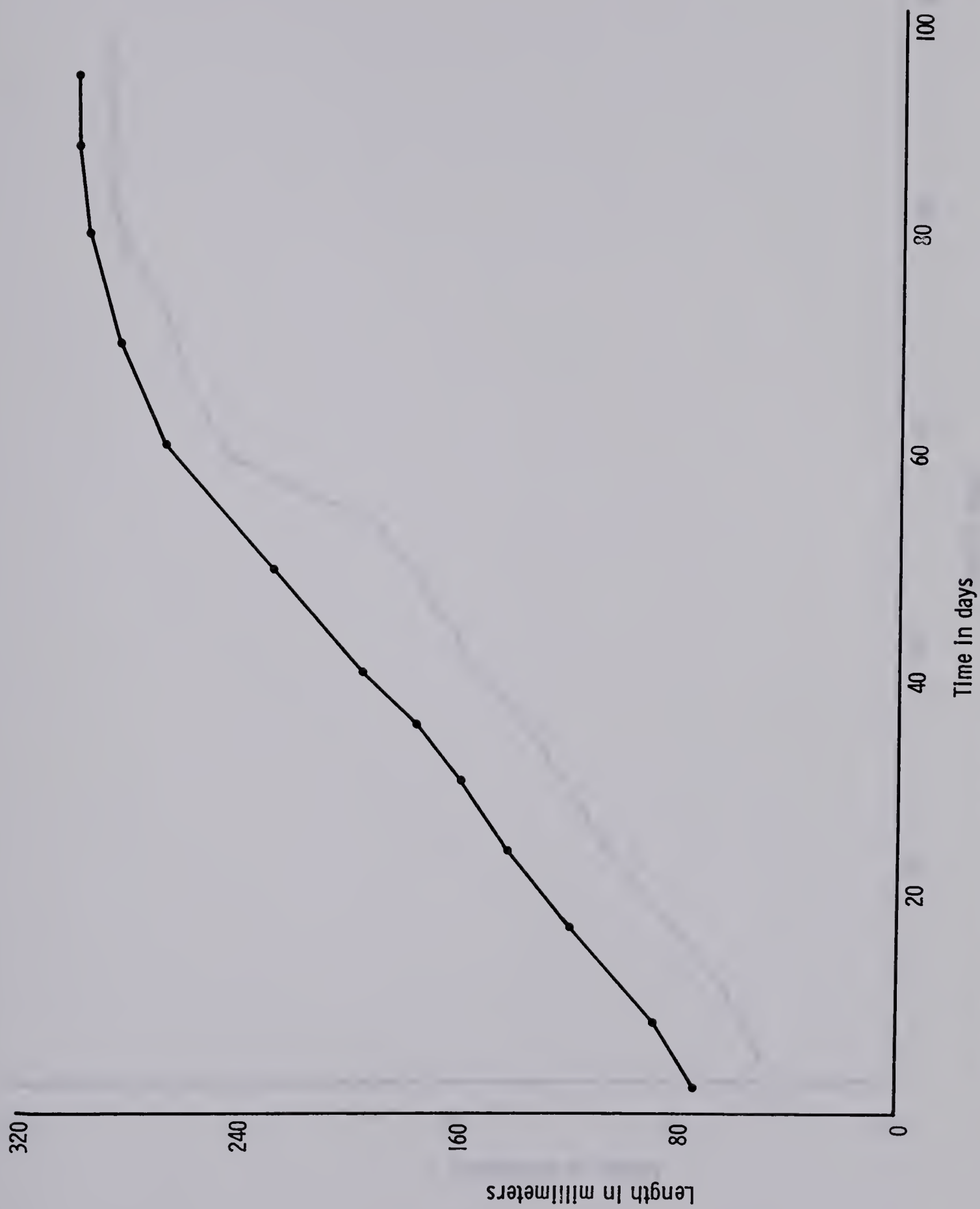


FIG. 4. Mean total length from day 2 to day 93.



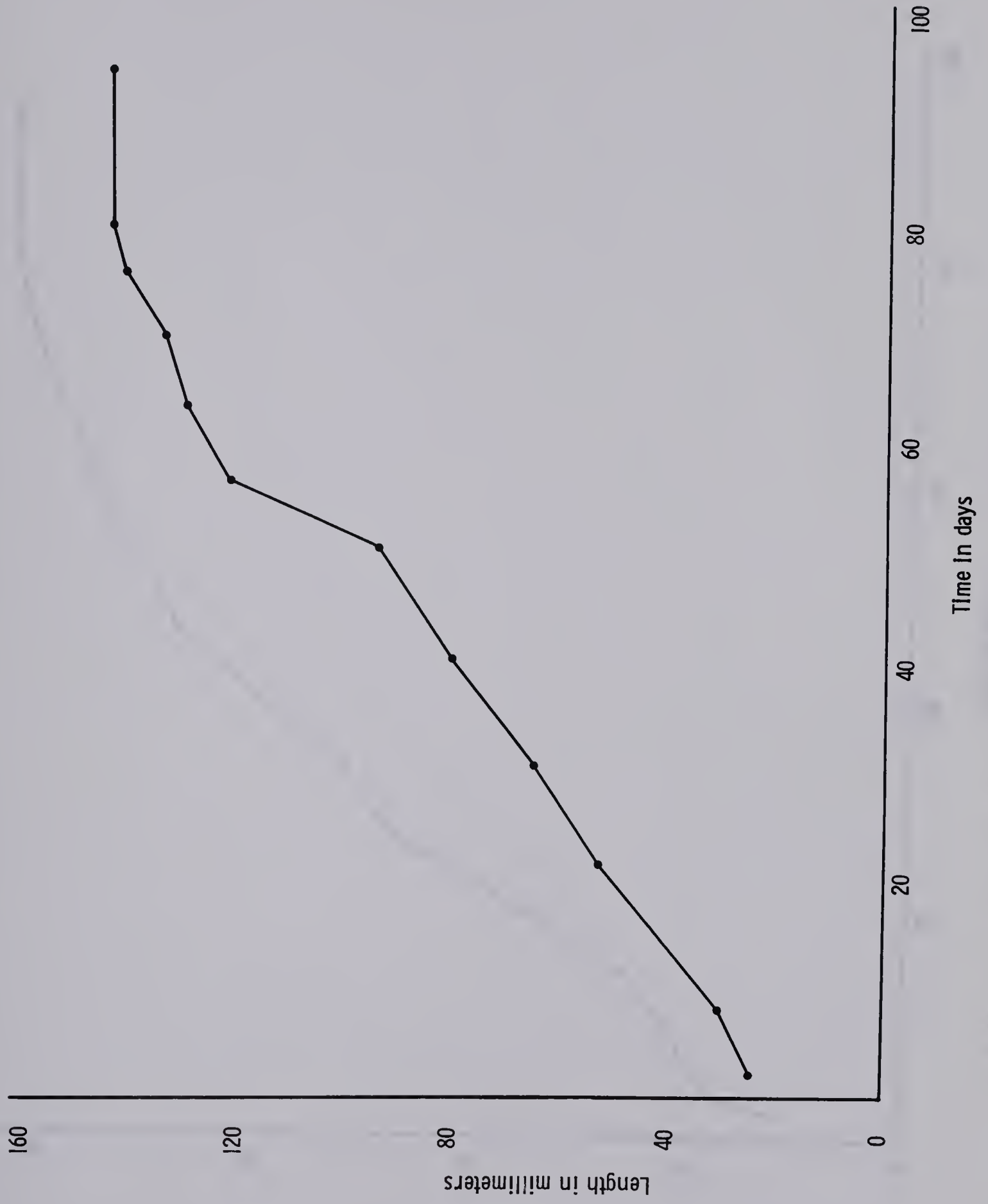


FIG. 5 Mean tail length from day 2 to day 93.





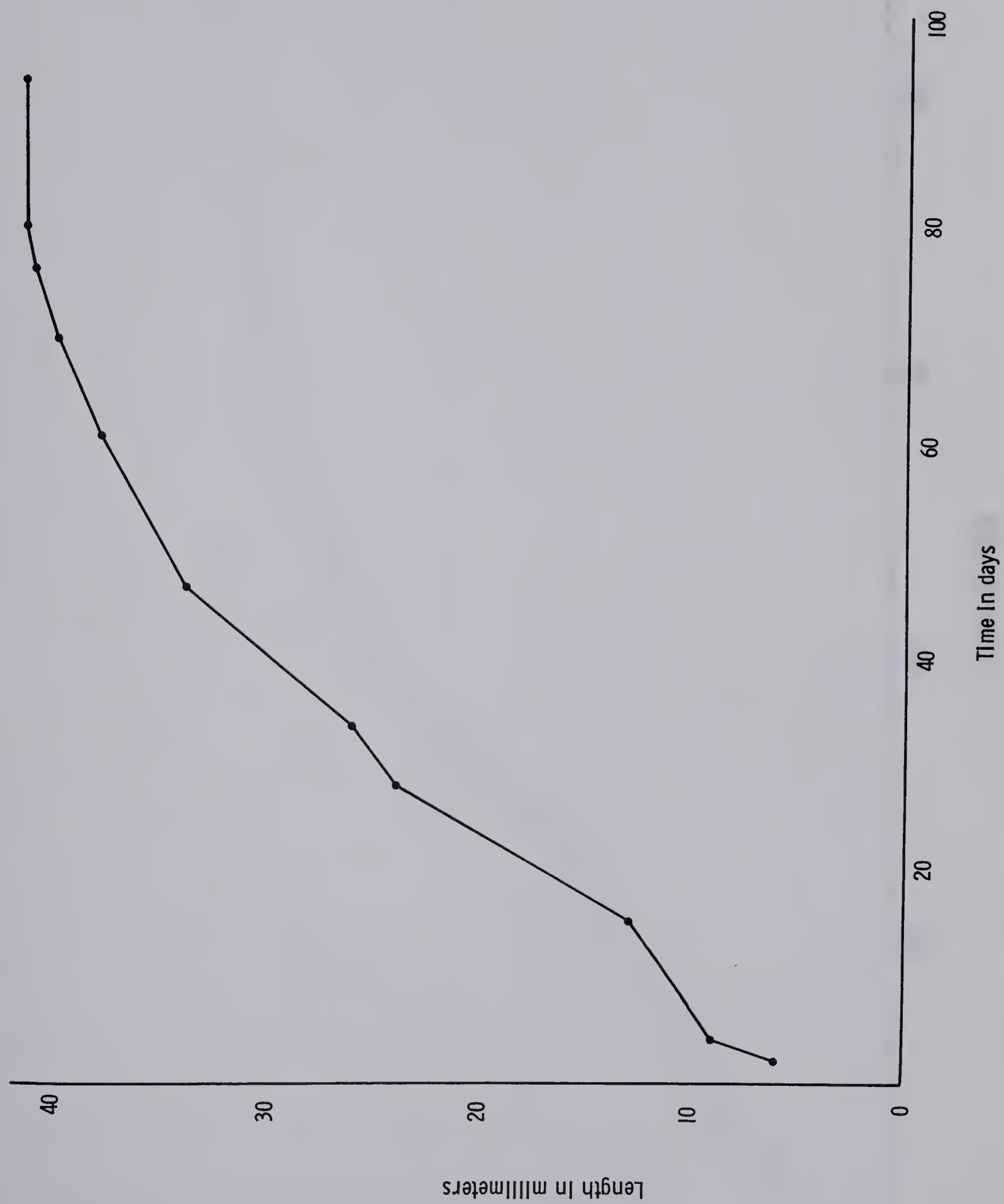


FIG. 6 Mean hind foot length from day 2 to day 93.



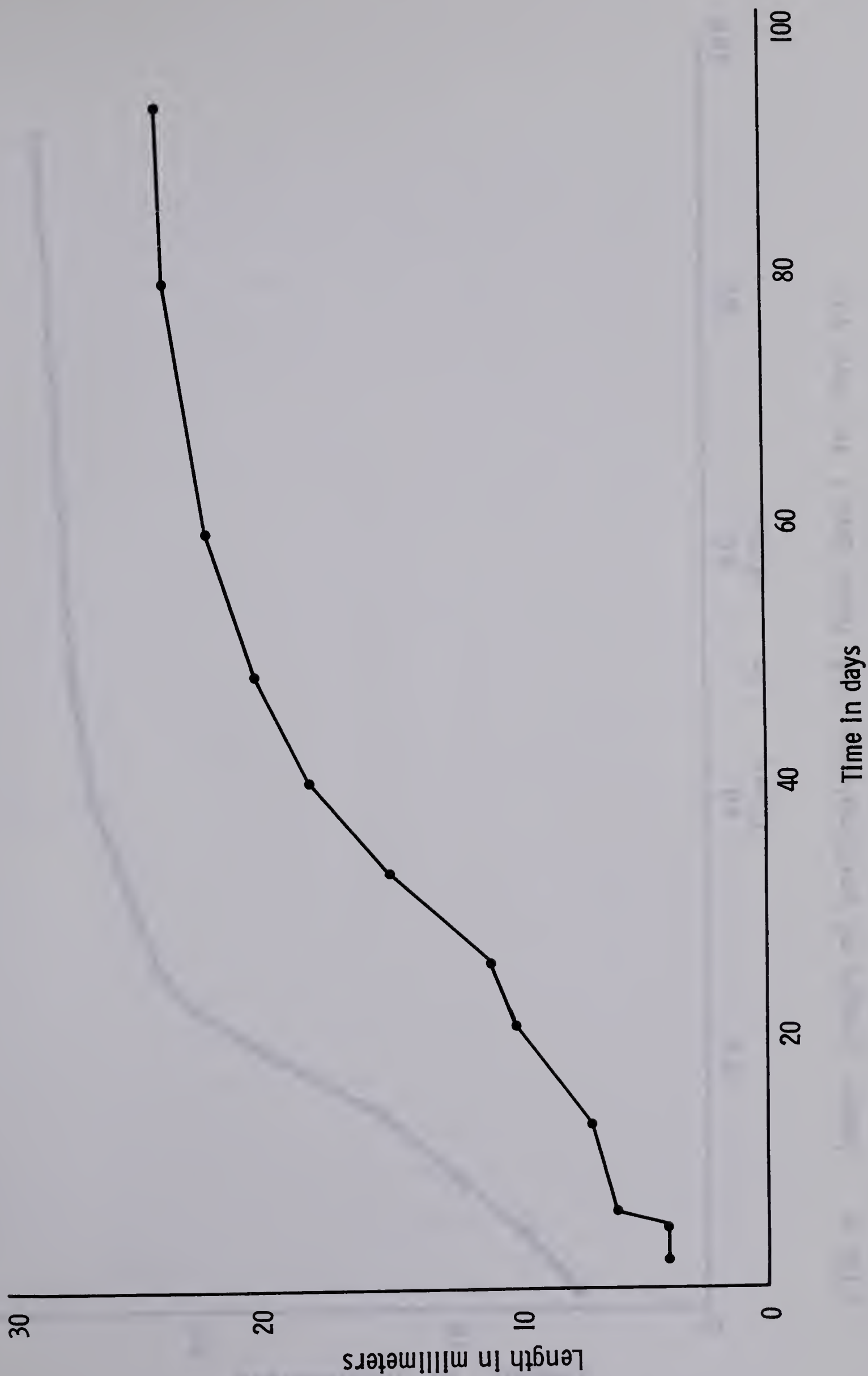


FIG. 7 Mean ear length from day 2 to day 93.





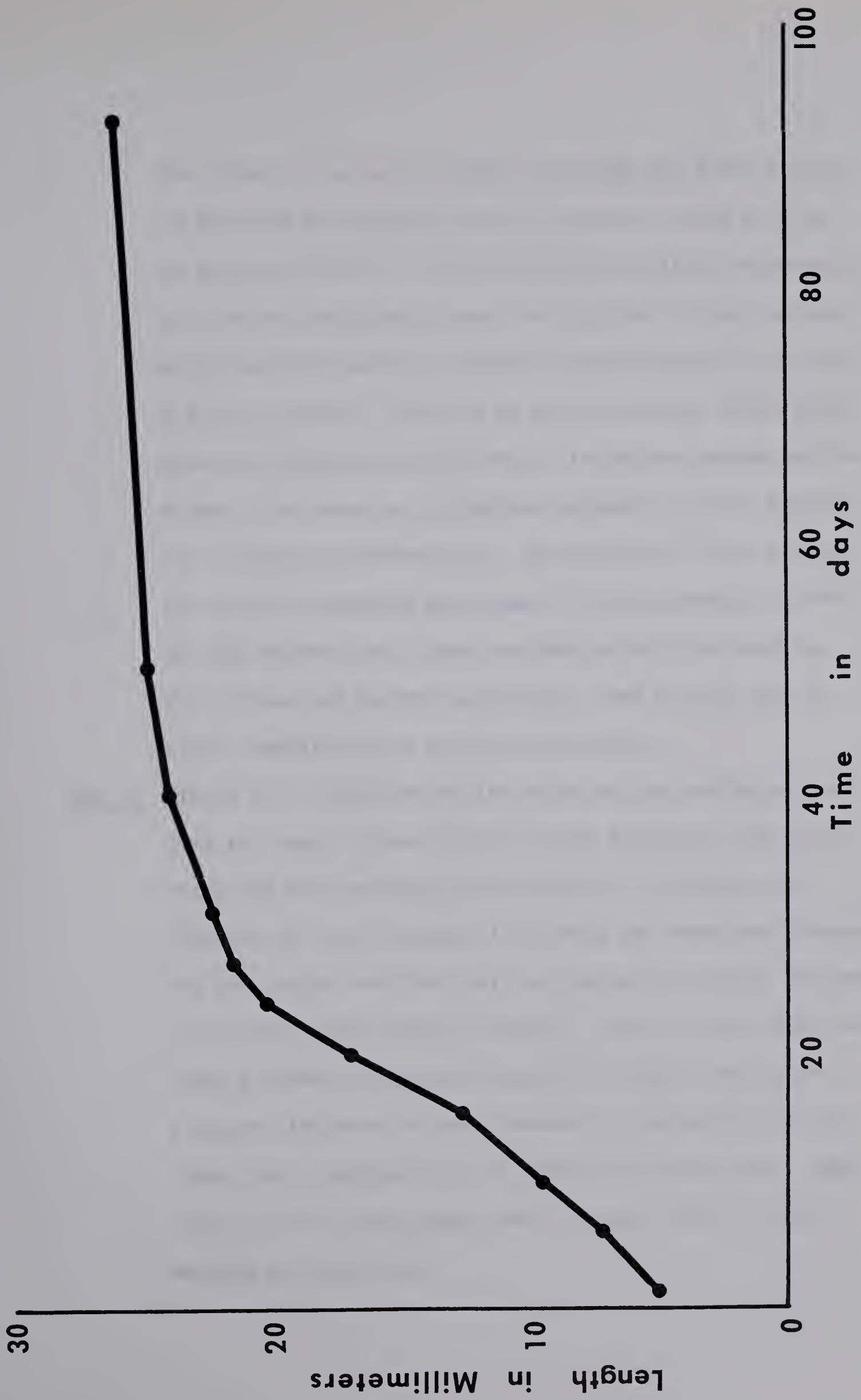


FIG. 8 Mean length of cartilaginous rod from day 1 to day 93.



The pinna of the ear is folded ventrally and fused closely to the head and measures 3 mm in greatest length by 2 mm in maximum breadth. A few fine white vibrissae measuring up to 1 mm in length are present on the sides of the rostrum, while the chin exhibits numerous fine white hairs less than 0.5 mm in length. The tail is round and blunt while claws measuring approximately 0.5 mm in length are present on the digits. The eyes are bulged and covered with skin bearing an ill-defined shallow slit. The young emit faint squeaking sounds resembling those made by humans drawing breath through pursed lips. They are able to hold the head up for 2-3 sec and squirm vigorously. They are not able to right themselves when placed on the back.

Day 2. (Plate 17). Vibrissae on the sides of the rostrum measure 3 mm in length. Young try to squirm forward on the belly using the feet and legs for propulsion. Sometimes the sequence of limb movements is lateral and sometimes diagonal, but more often the front pair are advanced together followed by the hind pair moving in unison. Once the hind limbs are under the body, the fore limbs are advanced. From this position, the mass is moved forward by the pulling of the front limbs combined with the push of the hind ones. However, the fore limbs appear much stronger than the hind members at this stage.



- Day 4. (Plate 18, top squirrel). Dark pigment beings to appear on crown and dorsal cervical region. The tip of the pinna breaks free from the head and unfolds through  $90^{\circ}$  until it stands out at right angles to the side of the head. The young are just able to turn over when placed on their back. With the rump as centre and propelled by the front limbs, the young squirrels circle either to left or right. Fore limbs are still obviously much stronger than hind ones as the latter tend to be dragged a good deal.
- Day 6. The ears have completely unfolded and are now closely appressed to the curvature of the skull, having unfolded through an angle of more than  $180^{\circ}$ . The young squirrels turn over more readily when placed on their back.
- Day 8. (Plate 18, middle squirrel). All the dorsal surface is pigmented except for the limbs and patagia. The pigmentat-  
ion on the dorsal surface of the tail is very faint, however. Fine dark fuzz covers the rostrum and the forehead from the tip of the nose to the base of the cervical region. The young cling to the finger when handled and are able to support the head in an upright position for extended periods.
- Day 12. (Plates 19 and 20). The entire dorsal surface of the body is pigmented but patagia and limbs only faintly darkened. Find golden pelage is present on the crown and the dorsal





region of the neck. The ventral surface is unpigmented although very fine white fur is present mid-ventrally from chin to base of thorax. The young progress backwards a good deal by pushing with the fore limbs. Vibrissae measure 11 mm and the eye-slit is more pronounced. When suspended in mid-air by the tail the young exhibit the spreading reflex in which limbs are fully extended thus spreading the patagia to maximum extent.

Day 15. The ventral tail surface is faintly pigmented and fine dark fuzz is present on its dorsal and lateral surfaces. The ventral surfaces of the patagia and inner surfaces of the limbs are naked and unpigmented. The distal portion of the pinna is no longer appressed to the head but stands out 1-2 mm from it.

Day 18. Thick golden pelage is present on the crown and dorsal cervical region. An admixture of brown and golden pelage extends dorsally from the base of the cervical region to the base of the tail. Buffy areas are present over the eyes and the eye-slit is much more prominent. The ventral surfaces are unpigmented except for the tail. The lower incisors protrude 3 mm from the gums but are covered with a thin transparent membrane.

Day 20. (Plate 21). Ventral surface of the lateral margins of the patagia is lightly pigmented. The entire ventral



surface is lightly furred except for the patagia and lower abdominal region. The external auditory meatus is now open. Eyelids are separated by a distinct narrow slit. The patagia hang in loose folds; the associated musculature is not yet functional.

Day 22. (Plates 22 and 23). The outer half of the ventral patagium is pigmented. The entire ventral surface is lightly furred with a pronounced area of white pelage running midventrally in the thoracic region. A "mask" of grey pelage extends around the eyes and over the top of the nose. The lower incisors have broken through the gum membrane. The young are more active and cling vigorously to the fingers when handled. They have begun to gather all four feet under the body while attempting to walk, but often lose their balance and fall over on their sides. They also attempt to move backward, pushing with the fore limbs. The young squirrels "start" markedly in response to sudden loud noises such as a hand-clap.

Day 24. The tail is covered with thick black pelage particularly on the dorsal and lateral surfaces and measures 8 mm in breadth at the widest point. Vibrissae are 20 mm in length. The patagia tend to be drawn in closer to the body rather than lying in loose folds around it, probably indicating the development of the associated musculature.





A narrow margin, 3 mm in width, along the lateral edges of the patagia is relatively lightly furred, and appears almost naked in comparison with the adjoining surfaces. The lower incisors extend 2 mm beyond the gum and are clearly visible for 3 mm below the surface. The young are able to hang upside down, clinging with all four feet to a horizontal branch, for a period of 3 sec before falling. They are also able to climb a few steps upward on a rough spruce log held at an angle of  $45^{\circ}$  with the horizontal. When placed upon a sloping surface they evince a marked tendency to climb upward rather than downward, utilizing a diagonal sequence of limb movements.

Day 26. (Plates 21 and 24). The entire dorsal surface is gold including 7 mm of the proximal end of the tail. Fine, white fur is present on the ventral surface to within 15 mm of the anus. The ventral surface of the patagia is dark grey. The patagia are drawn up at the sides and the tail is flattened. The young squirrels cling readily to the underside of a branch for periods up to 12 sec duration. The body tends to be closely appressed to the surface. The fore limbs appear much stronger than the hind ones and are able to cling for several seconds after the hind members have lost their grip.

Day 28. (Plate 25). Eyelids appear to be separating but the eyes



are not yet open. The dorsal surface of the lateral margins of the patagia exhibits fine, golden pelage.

Day 29. The first record of an individual with its eyes open.

The eyes are apparently not yet light sensitive since the squirrels do not turn away from a strong light placed at close range. They are very active, wriggling about the nest box a good deal.

Day 33. Upper incisors first appear. All individuals have the eyes open but not bulging.

Day 34. The young move about freely but make little use of the hind limbs for propulsion.

Day 38. The young begin to make use of the hind limbs to a limited extent while crawling about. They begin to climb the sides of the nest box and are able to cling for brief periods supported only by the fore limbs.

Day 40. Young are able to climb one's arm to the shoulder but are unable to descend. They can pull themselves up vertically using the front limbs. Hind limbs are apparently still relatively weak. They lap a mixture of canned milk and Pablum and suck on pieces of raw and canned fruit.

Day 43. Young begin to make short exploratory excursions from nesting box, but remain in close proximity to it.

Day 45. Young explore their surroundings at some distance from nesting box, and one individual climbed up a tree trunk for several





feet. They begin to gnaw on nuts, wood and pieces of apple, and their eyes are bulging much more prominently.

Day 49. They try, unsuccessfully, to sit on their haunches in order to free the fore limbs for food-handling. Finally, they prop themselves securely in a corner of the nest box and with this added support are able to sit upright while holding food in their fore paws.

Day 50. One individual jumped or fell from a table and spread the patagia before landing on the floor.

Day 58. Individuals are able to make 8-inch horizontal jumps from a branch to a tree-trunk after much head-bobbing. Patagia are not involved in such short jumps. They still attempt to suckle, and make "phut, phut" sounds resembling those of the adults. They are able to descend tree-trunk, head first, using the hind limbs for support, and sit unsupported while handling food with the fore paws.

Day 66. Young commonly make leaps of 2 to 3 ft, spreading the patagia fully.

Day 70. Young are able to glide 5 to 6 ft and land in characteristic attitude. The litters have begun to break up, with individuals of the same litter found sleeping in different nest boxes.

### Discussion

In general, the growth of the body parts investigated followed the growth pattern in animals outlined by Simpson et al (1957). Birth





is followed by a period of rapid growth which, in time, tends to give way to a period of tapering off. All of the graphs exhibit fluctuations in growth rates but the major deviations are usually explainable. Rates vary considerably from body part to body part. Hind foot and ear had attained near-maximum length by day 50 while tail and total body required 56 and 60 days respectively to reach about the same stage. On the other hand, body weight was not near maximum until day 142 and indeed continued to increase gradually for several more months. Simpson states that body weight in humans tends to increase until middle age.

Activity increases a good deal once the eyes are open. By this time, the fore limbs are quite well-developed and are capable of supporting the squirrel for brief periods as it clings to surfaces. At this time, the hind limbs are weaker than the fore limbs but in just over two weeks time are able to support the animals when sitting in an upright position. In another 10 days, the young squirrels are able to use the hind limbs for support when descending trees. Short jumps and glides are begun soon after hind feet and tail have reached near-maximum proportions.

Davis completed a study of the ecology of northern flying squirrels in Saskatchewan in 1963. During his study he obtained growth data for one litter of the species reared in captivity. In general, his squirrels were heavier at birth, approximating the weights of one of the litters included in this study in the section



related to general growth and development. Also, on the average, Davis's squirrels matured more rapidly than those for which rather complete data were secured in this study. His squirrels showed similar phases in weight gain but failed to record the drop in September observed in the squirrels in this study. While his animals registered more rapid gains in total length, the final means of both litters were within one millimeter of one another. While the mean hind foot length of Davis's squirrels reached near-maximum length in 43 days, the squirrels in this study required 50 days to reach the same point. While Davis's squirrels showed no increase in ear length from day 18 to day 25, the squirrels in this study exhibited steady, but somewhat reduced, gains over the same period. Davis (1963) states that ear length in his squirrels increased slowly until day 133; the squirrels studied in this project had attained adult ear lengths by day 79.

The differences are not great and might well have been due to such factors as diet, physical condition of the mother, laboratory conditions, etc.

Responses somewhat similar to that which I have termed the spreading reflex (Plates 19 and 20) are viewed in an interesting light by Dr. M.R.A. Chance of the Ethology Laboratory, Uffculme Clinic, Birmingham, England. In a brief personal conversation in July 1965, Dr. Chance hypothesized that somewhat comparable reactions in rats and mice are examples of convulsions. He does not feel that







all convulsions are pathological in nature but, rather, that such phenomena are often "built in" to small mammals where they may serve as escape mechanisms for the species concerned. It is not difficult to appreciate the survival value of such a response in a young flying squirrel when accidentally falling from a height.

PLATE 15

G. sabrinus in nest at age 7 hours.

The litter was born at approximately 10 AM on May 13, 1965. Note fused ears, wrinkled skin and eye-slit. The nest was composed mostly of shredded willow (Salix) bark along with dry grass (Agropyron, Bromus and Hordeum) and feathers.







PLATE 16

G. sabrinus at age 1 day. Dorsal view.

The skin is slack, translucent and unpigmented. Vibrissae measuring 1 mm are present on chin and sides of rostrum. Measurements are L.66-22-8-2N, 6.6 g. The cartilaginous rod attached to the pisiform bone measures 5 mm in length. Terminal claws measuring approximately 0.5 mm in length are present on the digits.

# Modern Tools of Science

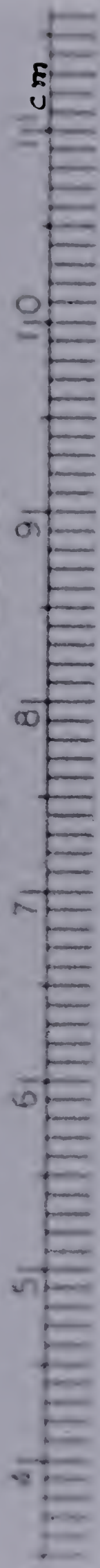




PLATE 17

G. sabrinus at age 2 days. Side view.

This is the same individual as in Plate 16.

The ears are tightly folded ventrally and fused to the head. A shallow eye-slit is present. The skin and patagia are very slack. X 2.65.



PLATE 18

G. sabrinus at ages 4, 8 and 10 days.

At day 4 (top squirrel) there is barely a suggestion of pigment on the crown of the head and dorsal shoulder region. Also, in this individual the tip of the right ear has broken free from the head but is still folded at right angles to it. The left ear is just starting to unfold. By day 8 (center squirrel) all the dorsal surface is pigmented except for the limbs and patagia. All ventral surface is unpigmented. Ears are erect but closely appressed to the head. Fine dark fuzz covers and rostrum and the forehead and extends dorsally from the tip of the nose to the base of the cervical region. The young at age 10 days (bottom squirrel) show little change from 8 days except that they are heavier and darker.



PLATE 19

Spreading reflex in G. sabrinus at age 12 days.  
Dorsal view.

When held suspended by the tail with head downward, the young squirrel immediately assumed this attitude with limbs extended and patagia taut. When held by the loose skin of the ventral or dorsal surface and either in horizontal position or with the head upward, the squirrel tended to draw the limbs in towards the body and arch the spine. Note the developing cartilaginous rod under the skin in the region of the right wrist. X 1.90.





PLATE 20

Spreading reflex in G. sabrinus at age 12 days.  
Ventral view.

When suspended in this fashion the squirrel spreads its limbs to maximum extent and in approximately the gliding position. Note tension on patagia. The subject is a young female. X 1.90.



PLATE 21

G. sabrinus at ages 20 and 26 days.

The patagium in the younger squirrel on the left tends to fall in loose folds indicating that the associated musculature is probably ill-developed and not yet functional. In the older squirrel, the patagium is somewhat retracted. Note also the difference in tail development.





PLATE 22

G. sabrinus at age 22 days.

The young squirrel is now able to gather its hind feet under the body when sleeping or attempting to walk. Previously, the hind limbs tended to project laterally in salamander fashion (see squirrel at age 20 days, Plate 21). Note the relatively naked dorsal margins of the patagia.



PLATE 23

G. sabrinus progressing backwards at age 22 days.

Note the characteristic attitude assumed by the young northern flying squirrel when progressing in a backward direction. The fore limbs are well under the body and appear responsible for most of the effort exerted. Head, neck and hind limbs tend to trail along the substrate contributing little propulsive force. The lumbar-sacral region is arched due to the friction of the posterior regions with the substrate, together with the direction of motion.



PLATE 24

G. sabrinus clinging to under side of horizontal branch at age 26 days.

Almost the entire ventral surface tends to be closely appressed to the surface of the branch. The relatively strong fore limbs grasp the bough securely. When falling from this position, the squirrel maintains its grip with the front feet for several seconds after the hind feet have lost their hold. On occasion, the young squirrel may maintain its grip with the fore limbs for a sufficiently long period to allow it to regain its hold with the hind limbs.





PLATE 25

G. sabrinus at age 28 days.

By this time the eye-lids appear about to separate, with their opposing margins clearly defined. The apex of the pinna is no longer appressed to the curvature of the skull. The young are able to pull themselves upward using the fore limbs as the major motive force.





PLATE 25A

Glaucomys sabrinus at age 33 days.

The eyes had opened 2 hr prior to the taking of this photograph. While the eye has not yet begun to bulge, by day 36 the curved cornea protrudes well beyond the eyelids. The tail is long, flattened and dark in color. The patagia are retracted at the sides. Shortly after the opening of the eyes there is a marked and increasing tendency for the young squirrel to progress in a forward direction rather than either backward or rotating about the pelvis.





PLATE 26

Female G. sabrinus carrying young at age two weeks.

When the females carry their offspring they usually grasp them by the slack skin of the thoracic region either dorsally or ventrally. Note the whitish scars in the dorsal thoracic region of the youngster in the foreground. It is common practice for the adult female, either in captivity or in the wild, to transfer her young to a new nesting site if disturbed.





## V. MORPHOLOGY INVESTIGATED

### Body Densities

It seemed a reasonable hypothesis that northern flying squirrels might have lower total body densities than squirrels which lack the capacity for sustained gliding. Accordingly, intact freshly killed specimens of Glaucomys sabrinus and Tamiasciurus hudsonicus were investigated as described in Chapter III. Tables 1 and 2 summarize the results obtained.

It is clear from an examination of the data in these tables that we are dealing with two distinct samples with respect to total body density. There is no overlap in the average body densities of the two species expressed in grams per cc; they are discontinuous. The specimens of Glaucomys sabrinus range from 0.74 grams per cc to 0.80 grams per cc with an average mean total density of 0.765 grams per cc. On the other hand, the specimens of Tamiasciurus hudsonicus range from 0.84 grams per cc to 0.90 grams per cc with an average mean total density of 0.878 grams per cc.

An "F" test gives a value of 1.70, showing that the standard deviations of the two samples do not differ by a statistically significant amount and hence could come from the same population. A "t" test gives a value of 3.74 while a "t" value of only 2.750 is required for a highly significant difference at the .01 level, with 30 degrees of freedom. Hence, the sample means could hardly come from the same population.





On the basis of these samples and with the limitations of the study in mind, it seems warranted to conclude that intact northern flying squirrels tend to be lighter, volume for volume, than intact red squirrels.

Earlier, somewhat casual density determinations had suggested that the previous statement might be true. Hence, in dealing with further samples, it was decided to measure the density of the freshly skinned body of each individual immediately after determining its total density. It was felt that this procedure might assist in isolating the factor, or factors, responsible for density differences should such differences, in fact, emerge. Accordingly, these measurements were made following the procedure outlined in Chapter II. Tables 3 and 4 summarize the results obtained.

A cursory examination of Tables 3 and 4 reveals the similarity of the samples dealing with the densities of the skinned bodies of the two species. While there is a marked tendency for individuals of each sample to cluster closely about the respective sample means, there is a good deal of overlap in the data. The specimens of Glaucomys sabrinus range from 0.98 grams per cc to 1.05 grams per cc with a mean density of 1.020 grams per cc while the specimens of Tamiasciurus hudsonicus range from 0.99 grams per cc to 1.06 grams per cc with a mean density of 1.026 grams per cc.

An "F" test, here, gives a value of 1.29 indicating that the samples are not significantly different even at the 0.1 level; the



standard deviations may well come from the same population. A "t" test gives a value of 0.62, indicating that the sample means are not significantly different even at the 0.5 level. Therefore, on the basis of these samples, again with the limitations of the study in mind, it seems safe to conclude that the skinned bodies of northern flying squirrels have approximately the same density as those of red squirrels; they are neither lighter nor heavier, volume for volume.

#### Skin Densities

Since the mean total density of intact northern flying squirrels proved lower than that for red squirrels, while the mean densities of the respective skinned bodies were approximately identical, the cause of the difference remained to be found. While the skin and pelage were evidently involved the difference could be simply due to the fact that flying squirrels, with their extensive patagia, have a good deal more cutaneous tissue than red squirrels. On the other hand, the nature of the respective cutaneous tissues might play an important role.

With these possibilities in mind, the densities of the skins of freshly killed specimens of both species were investigated. Results are given in Tables 5 and 6. The density of the skins of Glaucomys sabrinus ranges from 0.29 to 0.51 grams per cc with a mean density of 0.36 grams per cc. The density of the skins of specimens of Tamiasciurus hudsonicus, on the other hand, ranges from 0.35 to 0.57 grams per cc with a mean density of 0.45 grams per cc. A "t"





test gives a value of 1.12 indicating that the two sample means are not significantly different, even at the 0.2 level, and hence could come from the same population. Therefore the difference found in the intact specimens does not seem to be caused by differences in nature of pelage and cutaneous tissue. The important factor appears to be the differing amounts of these items possessed by members of the respective species.





Table 1. Densities of intact, freshly killed specimens of Glaucomys sabrinus measured during October, November and December, 1964.

Specimen No.	Sex	Dry Weight (grams)	Total Body Volume (cc.)	Density (grams/cc.)
67	M	118.4	154.5	0.77
68	F	172.0	231.1	0.74
69	M	118.6	155.8	0.76
61	M	185.5	244.2	0.76
70	M	183.7	237.3	0.77
52	F	223.7	280.6	0.80
71	F	137.5	177.4	0.78
72	F	106.8	153.2	0.76
73	F	186.1	250.3	0.74
51	F	186.0	238.3	0.78
201	M	187.1	246.1	0.76
202	F	187.3	253.2	0.74
210	M	135.0	171.0	0.79
211	M	154.3	207.5	0.74
44	M	162.5	206.5	0.79
212	M	156.2	196.2	0.79
213	M	142.4	183.4	0.77
48	F	259.0	326.0	0.79
49	M	158.9	212.9	0.74
53	M	138.6	184.9	0.75



Table 2. Densities of intact, freshly killed specimens of Tamiasciurus hudsonicus measured during December, 1964, and January, 1965.

Specimen No	Sex	Dry Weight (grams)	Total Body Volume (cc.)	Density (grams/ cc.)
101	M	233.2	264.1	0.88
102	F	206.4	231.0	0.89
107	F	164.2	188.6	0.87
108	M	193.3	214.9	0.90
105	F	199.2	233.2	0.85
109	M	226.2	253.2	0.89
110	M	187.2	208.6	0.90
111	F	195.3	219.4	0.89
112	M	218.5	243.1	0.90
113	F	214.0	257.4	0.84
114	F	193.4	221.2	0.87
115	F	169.2	195.8	0.86
116	M	192.0	217.2	0.88
117	M	188.6	217.8	0.87





Table 3. Densities of the freshly skinned bodies of specimens of Glaucomys sabrinus measured during October, November, and December, 1964.

Specimen No.	Sex	Dry Weight (grams)	Skinned Body Volume (cc.)	Density (grams/cc.)
67	M	99.2	101.5	0.98
68	F	134.4	131.3	1.02
69	M	99.8	97.6	1.02
61	M	149.5	144.7	1.03
70	M	148.3	144.3	1.03
52	F	186.3	185.1	1.01
71	F	111.0	108.7	1.02
72	F	86.7	86.0	1.01
73	F	144.0	143.6	1.00
51	F	151.6	152.2	1.00
201	M	150.4	148.3	1.01
202	F	151.3	144.2	1.05
210	M	117.0	112.6	1.03
211	M	129.4	124.3	1.03
44	M	139.1	134.5	1.03
212	M	127.3	130.8	1.03
213	M	122.6	119.1	1.03
48	F	197.0	193.3	1.02
49	M	130.0	128.7	1.00
53	M	117.0	111.5	1.05



Table 4. Densities of the freshly skinned bodies of specimens of Tamiasciurus hudsonicus measured during December, 1964 and January, 1965.

Specimen No	Sex	Dry Weight (grams)	Skinned Body Volume (cc.)	Density (grams/cc.)
101	M	193.2	193.4	1.00
102	F	178.2	180.1	0.99
107	F	140.6	135.4	1.04
108	M	166.2	161.0	1.03
105	F	176.8	178.0	0.99
109	M	191.5	182.1	1.05
110	M	164.4	158.7	1.03
111	F	170.2	162.3	1.04
112	M	191.6	181.4	1.06
113	F	186.1	178.3	1.04
114	F	168.7	168.5	1.00
115	F	150.2	143.2	1.05
116	M	164.7	160.9	1.02
117	M	163.6	161.1	1.02



Table 5. Densities of the skins of freshly killed specimens of Glaucomys sabrinus measured during October, November, and December, 1964.

Specimen	Sex	Dry Weight of Skin (grams)	Volume of Skin (cc.)	Density of Skin (grams/cc.)
67	M	19.2	53.0	0.36
68	F	37.6	99.8	0.38
69	M	18.8	58.2	0.32
61	M	36.0	99.5	0.36
70	M	35.4	93.0	0.38
52	F	37.4	95.5	0.39
71	F	26.5	68.7	0.38'
72	F	20.1	67.2	0.30
73	F	42.1	106.7	0.40
51	F	34.4	86.1	0.40
201	M	36.7	97.8	0.37
202	F	36.0	109.0	0.33
210	M	27.0	58.4	0.46
211	M	24.9	83.2	0.29
44	M	23.4	72.0	0.33
212	M	25.4	68.9	0.37
213	M	19.8	64.3	0.31
48	F	62.0	122.7	0.51
49	M	28.9	84.2	0.32
53	M	21.6	63.4	0.32





Table 6. Densities of the skins of freshly killed specimens of Tamiasciurus hudsonicus measured during December, 1964 and January, 1965.

Specimen No.	Sex	Dry Weight of Skin (grams)	Volume of Skin (cc.)	Density of Skin (grams/cc.)
101	M	40.0	70.7	0.57
102	F	28.2	50.9	0.55
107	F	23.6	53.2	0.45
108	M	27.1	53.9	0.50
105	F	22.4	55.2	0.40
109	M	34.7	71.1	0.48
110	M	22.8	49.9	0.45
111	F	25.1	57.1	0.44
112	M	26.9	61.7	0.44
113	F	27.9	79.1	0.35
114	F	24.7	52.7	0.45
115	F	19.0	52.6	0.36
116	M	27.3	56.3	0.48
117	M	25.0	56.7	0.44



### Surface Area of Patagia

The surface area of the patagia of specimens of G. sabrinus was investigated as outlined in Chapter II. Plate 27 taken at 1/5000 second, illustrates a characteristic attitude of the species assumed during gliding, while Fig. 9 indicates the manner in which specimens were pinned out on graph paper in order to estimate the ventral surface area of the patagia. The results are summarized in Table 7.

Ventral surface areas of the patagia of specimens studied varied from 23.44 to 29.96 sq in, with a mean area of 27.72 sq in. The percentage increase in ventral surface area due to patagia varied from 72.6 to 81.7%, with a mean increase of 77.2%. The mean for females was only slightly less than that for males.

### Surface Area of Tail

The surface area of the tail of specimens was examined as outlined in Chapter II. Results are summarized in Table 8. Ventral tail surface areas of the sample varied from 9.30 to 12.60 sq in with a mean area of 10.88 sq in. The ventral tail surface varied from 13.3 to 20.2% of total ventral surface area with a mean of 17.2%.





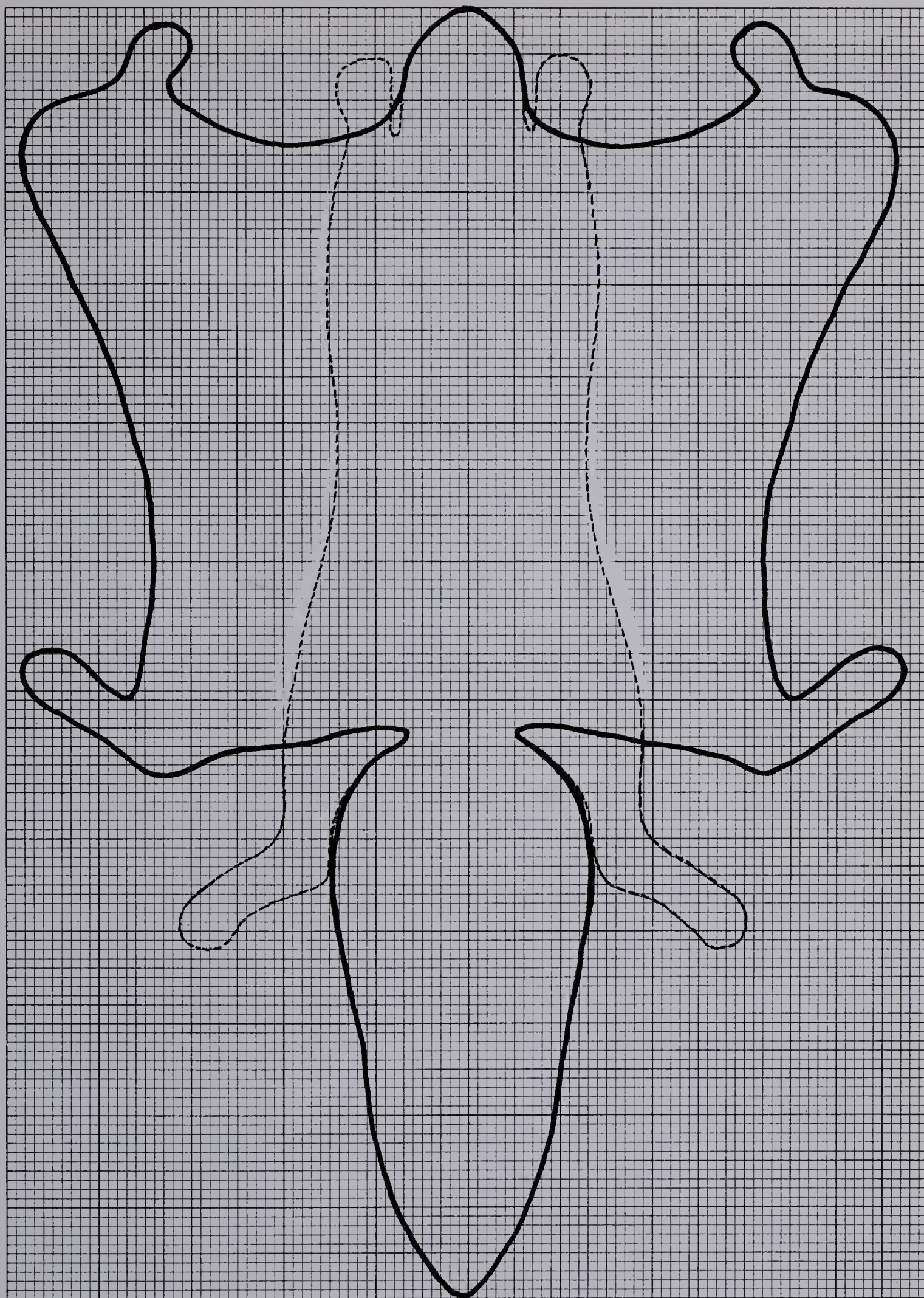


FIG. 9 Ventral surface areas of the northern flying squirrel.

PLATE 27

G. sabrinus in gliding position overhead.

The fore paws have been rotated so that the palmar surfaces are outward and digit V upward, while the hind paws have been turned outward with the plantar surfaces downward. A relatively rigid fold, part of the propatagium, stretches from the base of the head to the wrist. The cartilaginous rod is abducted and the patagia fully extended. A few feces cling to the pelage in the anal region. The squirrel is just passing out of the frame.







Table 7. Ventral surface area of patagia in Glaucomys sabrinus.

Specimen No	Sex	Ventral Surface Area (patagia spread) in <sup>2</sup>	Ventral Surface Area (patagia relaxed) in <sup>2</sup>	Ventral Surface Area of Patagia in <sup>2</sup>	Percentage Increase in Ventral Surface Area due to Patagia
67	M	60.70	34.08	26.62	78.1
68	F	62.48	35.04	27.44	78.3
69	M	61.08	34.78	26.30	75.6
61	M	69.72	39.76	29.96	75.3
70	M	65.12	35.98	29.14	80.9
52	F	70.12	40.62	29.50	72.6
71	F	60.82	34.42	26.40	76.7
72	F	55.64	32.20	23.44	72.8
73	F	63.48	35.30	28.18	79.8
51	F	64.86	36.46	28.40	77.9
308	M	65.68	36.14	29.54	81.7





Table 8. Ventral surface area of tail in Glaucomys sabrinus.

Specimen No	Sex	Total Ventral Surface (in <sup>2</sup> )	Ventral Tail Surface (in <sup>2</sup> )	Ventral Tail Surface/Total Ventral Surface (%)
67	M	60.70	10.96	18.1
68	F	62.48	12.60	20.2
69	M	61.08	10.34	16.9
61	M	69.72	12.04	17.3
70	M	65.12	10.14	15.6
52	F	70.12	9.30	13.3
71	F	60.82	12.22	20.1
72	F	55.64	10.76	19.3
73	F	63.48	9.84	15.5
51	F	64.86	10.08	15.5
308	M	65.68	11.36	17.3



### Supporting Cartilaginous Rod

The anterior corner of the plagiopatagium is partially supported on its lateral margin by a substantial cartilaginous rod (Plates 28 and 29, Table 9). In the newly born flying squirrel, this rod is only about 5 mm in length and very soft. However, in 21 adults the length of the rod ranged from 25 to 30 mm in length with a mean length of 28.5 mm.

Fig. 10 serves to clarify the relationship of the cartilaginous rod to other fore limb elements and the mode of its activation. The rod articulates firmly with the pisiform bone by means of a pronounced facet. As in the rat, the flexor carpi ulnaris muscle inserts on the pisiform. Hence, when this muscle is contracted the rod is adducted via the pisiform.

Abduction of the rod is more complicated. Here, a tendon from the extensor radialis brevis muscle passes first to a sesamoid bone deeply imbedded in the thick pad at the base of the vestigial thumb. From this sesamoid bone a ligament crosses the palmar surface of the carpals to insert on the lateral margin of the base of the cartilaginous rod. When the extensor radialis brevis contracts the rod is abducted. In the northern flying squirrel, the tendon from the extensor radialis longus muscle appears to split thus serving both the second and third metacarpal. Further abduction of the rod is accomplished by rotation of the manus into a vertical position





with the index finger downward. From this position, the squirrel then bends the wrist towards the mid-line exerting increased tension on the tendon leading from the extensor radialis brevis and thus abducting the rod still farther (Frontispiece and Plate 27).



Table 9. Length of supporting cartilaginous rod attached to the pisiform bone in Glaucomys sabrinus.

Specimen No	Sex	Age (Months)	Weight (grams)	Length Cart. Rod (mm)
67	M	4-5	118.4	25
68	F	4-5	172.0	27
69	M	4-5	118.6	28
61	M	12 plus	185.5	29
70	M	12 plus	183.7	29
52	F	17-18	223.7	28
71	F	4-5	137.5	28
72	F	4-5	106.8	26
73	F	4-5	186.1	30
51	F	24 plus	186.0	25
201	M	18 plus	187.1	29
202	F	12 plus	187.3	28
203	F	9	126.6	27
204	F	9	159.6	30
205	F	9	140.4	30
206	F	9	150.6	29
57	M	22	148.8	28
59	F	58	162.8	30
60	M	58	243.7	30
210	M	12	135.0	28
211	M	12	154.3	28
44	M	18 plus	162.5	29
212	M	12	156.2	30
213	M	12	142.4	26
48	F	24 plus	259.0	29
49	M	24 plus	158.9	27
53	M	24	138.6	28



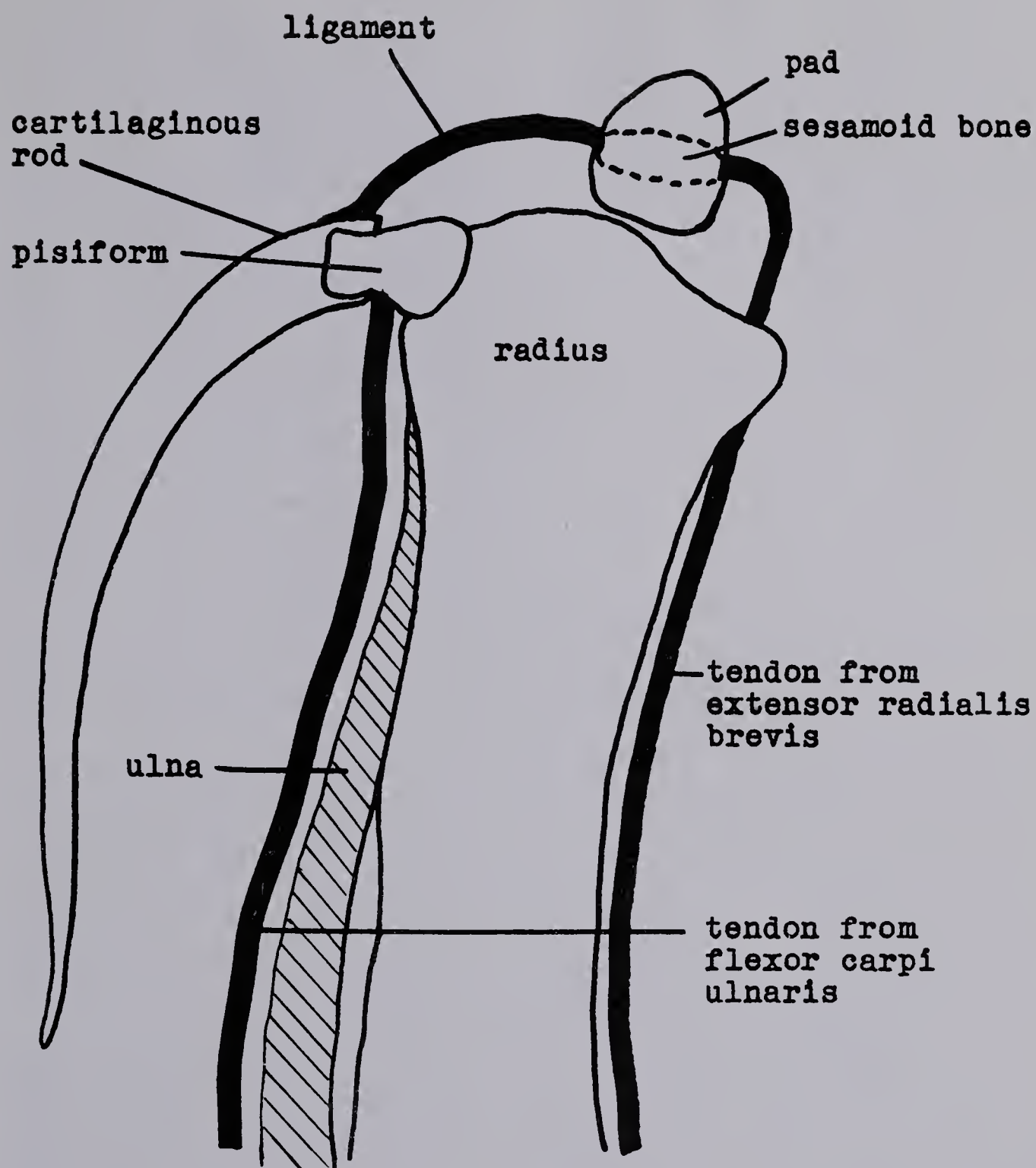


FIG. 10 Diagram of cartilaginous rod and associated structures in the right forelimb of Glaucomys sabrinus. Ventral view.



PLATE 28

Left fore paw of G. sabrinus. Ventral view.

Since the thumb is vestigial, northern flying squirrels possess but four functional digits on the front feet. The feet are equipped with extensive fatty pads while each functional digit has a stout terminal claw. The cartilaginous rod is clearly visible under the skin to the right. X 4.0



PLATE 29

Excised cartilaginous rods of G. sabrinus.

The rods depicted have been removed from the left fore limbs of individuals and preserved in 10% formalin. The mean length of this rod in 21 adults was 28.5 mm.







## Discussion

Northern flying squirrels possess a number of interesting morphological adaptations associated with their habit of gliding. They have a slightly lower total density when compared with a non-gliding relative, Tamiasciurus hudsonicus. Propatagia extend from the base of the head to the wrist on either side. When the squirrel is gliding, the anterior margin of the propatagium folds back on itself ventrally thus contributing a relatively rigid leading edge as in the wing of a bird when serving as an aerofoil. Extensive plagio-patagia extend on either side from wrist to ankle. These, together with the propatagia, appreciably increase the ventral surface area presented to the air, the most demanding medium in which to manoeuvre. Young (1962) states that flight necessitates a large surface/weight ratio; such a relationship would most certainly hold for efficient gliders. Soaring birds, flying bats and insects, gliding marsupials, anomalurids and dermopterans all possess adaptations which increase the surface area presented to the air when utilizing this medium for locomotion. Extinct pterosaurs possessed wings for this purpose while modern hominids make use of fabricated parachutes and winged aircraft of various designs

Control of the patagia is important. This is achieved in northern flying squirrels by the action of the limbs to which the patagia are attached as well as by the well-developed cartilaginous rod associated with each fore limb. In general, the patagia are



spread when the limbs are extended, while the cartilaginous rod exerts additional control of tension once the animal is gliding. The rod is activated by opposing musculature as well as by rotation of the manus into a vertical position with the index finger downward. In the genera Anomalurus and Idiurus, the patagia are partially supported by a cartilaginous spur projecting from the elbow; I am not aware that the activation of the spur in these genera has been worked out.

A stabilizer is essential and this is provided by the well-developed flexible tail characteristic of the species. The tail averages approximately 17% of the total surface area and since it is greatly flattened dorso-ventrally one would suspect that its chief purpose is to act as a stabilizer in the control of pitch. That the tail serves in other capacities with respect to balance seems clear from the accompanying motion picture film.

In addition, the relative lightness of the total animal should contribute buoyancy, an important feature in organisms and machines which engage in slow flight.

Wing-loading in 11 specimens of G. sabrinus varied from 3.1 to 5.1 kg/m<sup>2</sup> with a mean of 4.05 kg/m<sup>2</sup>. This compares with means of 20, 10, 3 and 1 kg/m<sup>2</sup> in the swan (Cygnus), duck (Anas), crow (Corvus), and goldcrest (Regulus) respectively (Young, 1962). On this basis, wing-loading in northern flying squirrels tends to be high. Since lift and drag vary with the product of wing area and the square of the speed, it would appear necessary for members of this species to attain relatively high speeds in order to obtain sufficient lift for planing.





## VI. PROGRESSION UPON HORIZONTAL SURFACES

### Walking.

Except when foraging casually for food upon the ground or when slowly descending a tree-trunk, adult northern flying squirrels were rarely observed to resort to the walking gait. When walking, support alternates either between three and four feet as in the juveniles or consists of phases in which two, three or four feet are in contact with the ground at a time. Progressing from left to right and using circles to represent specific feet upon the ground at any one time, the successive phases of the walk of the adults might be represented as follows:

$\begin{array}{c} \circ \\ \text{---} \circ \end{array}$    
 $\begin{array}{c} \circ \\ \circ \text{---} \circ \end{array}$    
 $\begin{array}{c} \circ \\ \circ \text{---} \circ \end{array}$    
 $\begin{array}{c} \circ \\ \text{---} \circ \end{array}$    
 $\begin{array}{c} \circ \\ \circ \text{---} \circ \end{array}$    
 $\begin{array}{c} \circ \\ \circ \text{---} \circ \end{array}$    
 $\begin{array}{c} \circ \\ \circ \text{---} \circ \end{array}$    
 $\begin{array}{c} \circ \\ \text{---} \circ \end{array}$

Support by two hind feet and one front foot is often prolonged as the squirrel holds the other front foot in the air with digits doubled for periods of from one to three seconds. The squirrels were using the lateral sequence diagonal couplets support patterns of Hildebrand (1963).

The crawling walk of Howell (1944) was found to be common in juveniles beginning with rather uncoordinated attempts on the first day after birth. Here, the lateral sequence of limb movements is favored with support by three feet alternating with support by four feet. Beginning with the left front foot, the sequence of footfalls is right hind, right front, left hind, left front. Using the method outlined above, the crawling walk of juvenile northern flying squirrels might be represented as follows:

$\begin{array}{c} \circ \\ \text{---} \circ \end{array}$    
 $\begin{array}{c} \circ \\ \circ \text{---} \circ \end{array}$    
 $\begin{array}{c} \circ \\ \circ \text{---} \circ \end{array}$    
 $\begin{array}{c} \circ \\ \circ \text{---} \circ \end{array}$    
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 $\begin{array}{c} \circ \\ \circ \text{---} \circ \end{array}$    
 $\begin{array}{c} \circ \\ \circ \text{---} \circ \end{array}$    
 $\begin{array}{c} \circ \\ \circ \text{---} \circ \end{array}$





### Trotting

Trotting was observed only when the squirrels were progressing along slender branches and occurred both when the animals were right side up and when they were upside down. Here the diagonal limbs move in pairs, the pairs alternating with one another. No period of total suspension was observed since one pair of diagonals tends to make contact with the running surface before the other pair leaves. The trot is occasionally transitional between the walk and the bound.

### Running

When progressing rapidly upon horizontal surfaces northern flying squirrels tend to resort to either the bound or half-bound. The former is characterized by movement of both front and hind limbs in a paired fashion while in the latter the hind limbs act in unison but the front ones are set one ahead of the other in time and space. The half-bound is commonly used by hares at all rapid speeds. These animals leap from the paired hind feet and land first upon one of the fore feet before quickly shifting their weight to the other front foot. The tracks which they leave in the snow are clearly indicative of this gait. Weasels, on the other hand, commonly use the bound, setting their paired hind feet in the tracks left by the paired front ones. Occasionally, however, northern flying squirrels were observed to utilize the gallop but the gallop in question was very close to the half-bound in that the sequence of the hind feet was very closely spaced.



The sequence of events in the bound or half-bound as utilized by northern flying squirrels is interesting. The leap is made from the widely spread hind feet in plantigrade position and well forward under the body. In this position the spine is markedly arched due to the extreme forward position of the hind limbs. The fore feet have already left the running surface and are closely appressed to the ventral surface of the squirrel with the palmar surfaces facing upward. The fore limbs now begin swinging forward through an angle of approximately  $180^{\circ}$  to take up a horizontal position under the chin. The body is propelled forward and upward with the straightening of the powerful hind limbs. As the squirrel leaves the running surface for the first, and relatively long, period of suspension the arch of the back levels out and the hind feet trail. The hind feet, initially far apart, swing towards the midline and their plantar surfaces rotate into a position facing one another. The squirrel then lands either upon both front feet simultaneously or briefly upon a single front foot prior to bringing the other down. At this stage the body is inclined to the running surface with the posterior end slightly raised which provides room for the ensuing movement of the rear limbs. The hind feet now begin to move away from the midline and accelerate with respect to the rest of the body, passing forward and outside the front limbs. Thus there is a minimum of interference between fore and hind pairs.

As the hind feet pass forward and around the front feet, the







spine again develops a decided arch. The front feet pull the body forward and upward briefly and then leave the running surface just prior to the contact of the hind feet with the ground. For this reason the squirrel experiences a second, but brief, period of total suspension during the one stride. This second period of suspension is necessitated by the fact that though the front limbs have passed through an arc of approximately  $180^{\circ}$ , they are considerably shorter than the hind limbs and therefore incapable of swinging through an equal distance.

The arching of the back considerably lengthens the stride and at the same time brings the hind legs into a position well under the body where they are better able to exert force to the mass in a forward and upward direction. It is important to note that the subsequent lengthening of the body all occurs while the hind feet are in contact with the running surface (Plate 34). This means that practically all increase in body length occurs in a forward direction, thus increasing the effective length of stride which, in turn, increases velocity. In the northern flying squirrel this increase amounts to approximately one inch per stride.

Naturally, the body tends to fall during periods of total suspension. Partial recovery is made when shoulders and hips pass over the respective pair of feet; the remainder is accomplished by the powerful thrust of the hind limbs. Although one might expect the body to rise and fall a good deal during such progress, this action appears to be minimized by the flexing of the wrists and ankles. Most



of the energy exerted is converted to forward motion. Plate 30 gives a fair idea of the body trajectory of the northern flying squirrel while bounding.

Many hundreds of recorded bounds of northern flying squirrels varied in length from less than a foot to an extreme of 6.13 ft. The latter was more than twice the mean and occurred under particularly favorable conditions. The underlying snow had been heavily crusted just prior to a very light snowfall giving the wild squirrel a firm grip on the substrate and very little interference. In soft snow the bounds tended to average approximately 2.5 ft in length.

While the sequence of footfalls of the fore feet may be maintained during a series of bounds, they may also be reversed. This is illustrated in the accompanying motion picture film as well as in Plates 47 and 48. Both of these plates illustrate half-bounds which are very nearly full bounds. In Plate 47 the hind feet make contact together well in front of the fore feet but the left front foot touches down just ahead of the right member. Plate 48 is a photograph of the next impression in the series and shows a reversal of the order of front footfalls. Plate 46 illustrates the characteristic impressions of the half-bound; the imprints of the fore feet are decidedly spaced in the direction of travel while the imprints of the hind feet are paired.

Fourteen running rates of northern flying squirrels using the bounding gait ranged from 367 to 533 ft per min with a mean of 444 ft





per min. The highest speed recorded was therefore approximately 6.1 miles per hour. It must be borne in mind, though, that these squirrels were bounding along the surface of a narrow log (in order to keep them in focus) and that running room was restricted. The mean length of stride was only 11.4 in; the species experiences no difficulty in tripling this stride length under favorable conditions. It is felt that the above rate does not give much indication of the capability of northern flying squirrels under natural conditions. There seems little doubt that greatly increased stride length could materially add to the velocity of the squirrel. The grey squirrel, Sciurus carolinensis has been recorded running along the ground at 15 and 18 miles per hour (Shorten, 1954).

A limited number of runs of the southern flying squirrel, Glaucomys volans, gave running rates ranging from 408 to 555 ft per min with a mean of 471 ft per min. While the stride here dropped off to a mean length of 8.1 in, the rate of stride more than compensated, giving a mean velocity a little higher than that of the larger northern flying squirrel. The southern flying squirrels appeared to find the limited space less restricting. As well, it is known that larger muscles generally contract more slowly than smaller ones (Hill, 1956).

### Scent Trails

When introduced to new surroundings northern flying squirrels tend to explore the area cautiously before moving about freely. The initial ventures from the nest box are limited in extent and





interrupted by frequent returns to it. However, they gradually increase their sphere of activity as they familiarize themselves with the area. When new running and climbing surfaces are provided, the squirrels lay scent trails upon them before utilizing them in an uninhibited fashion. Scent trails are laid by depositing droplets of urine at intervals varying from two to seven inches. While doing this, the squirrel draws the hind feet forward, arches the back and erects the proximal portion of the tail, bringing the genital region into contact with the new surface (Plate 45).

The laying of scent trails probably has important survival value for the species. When venturing from the nesting site, familiar routes can be laid out progressively, thus facilitating swift retreat to the safety of the home cavity. The individual flying squirrel which utilized our feeding station so often, tended to use almost the identical route on every occasion observed. One was reminded of the path-habits developed by the water shrew (Neomys fodiens) described by Lorenz (1957).

Apparently Glaucomys sabrinus is not the only member of the Petauristinae recorded as laying scent trails in this manner. Liat (1965), writing of a captive Petinomys genibarbis malaccanus, reports that ".....upon releasing it in the hall at about 8-9 PM it hopped around the hall urinating as it went along."

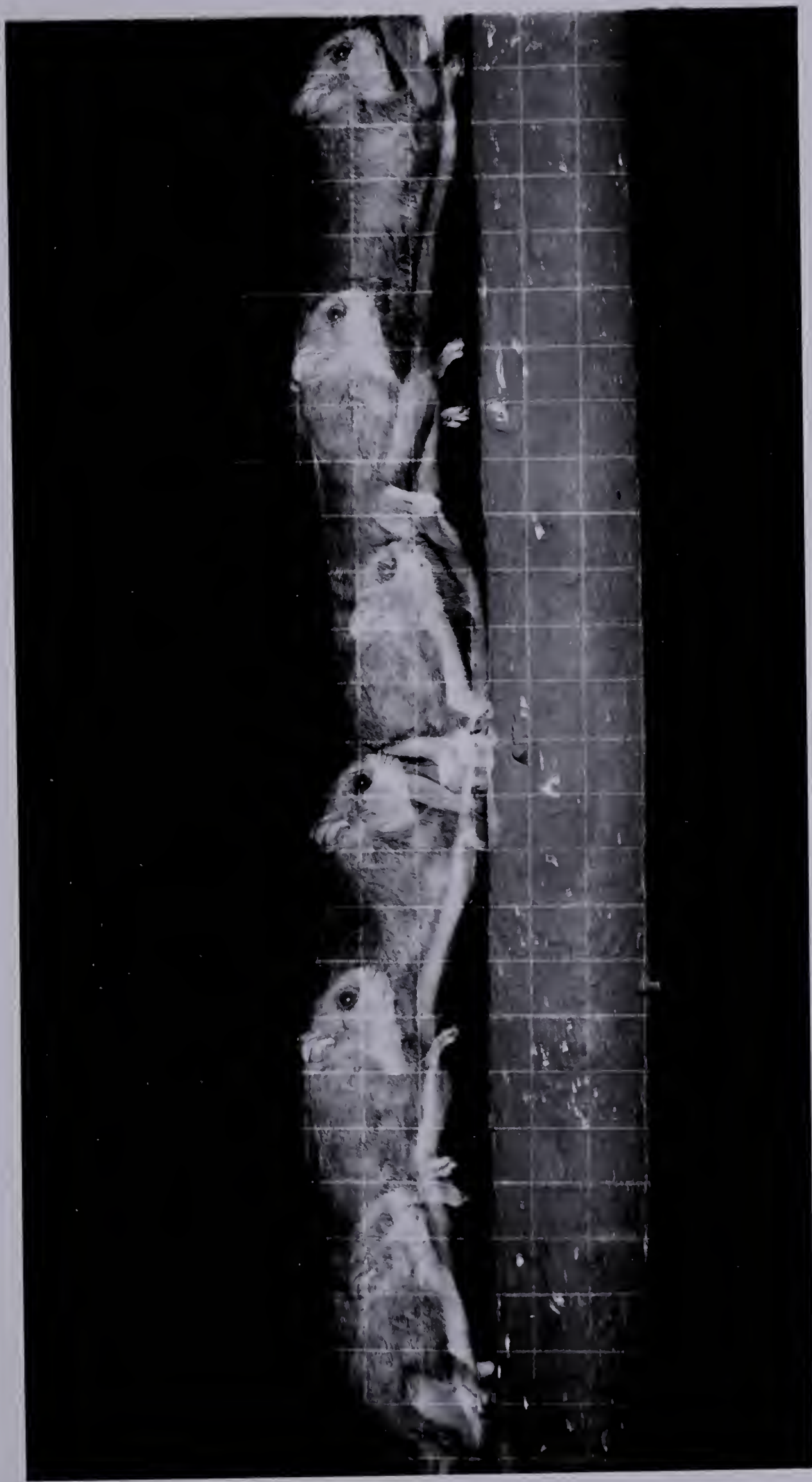
PLATE 30

Running trajectory of the northern flying squirrel.

Subject and grid at 4 ft.

Strobolume at 1200 cpm. High intensity.

Note the regularity of rise and fall of the subject  
and that most of the motion occurs in a forward direction.



Description of running plates

Plates 31 to 44 represent successive phases of the bound or half-bound characteristic of the northern flying squirrel while running. Plates 50 to 58 illustrate somewhat comparable running phases of the southern flying squirrel and are included for purposes of comparison. All photographs were taken at 1/5000 sec with Dormitzer Synctron high-speed electronic flash. The grid behind was calibrated in inches.

PLATE 31

Early bounding phase.

The entire plantar surfaces of the paired hind feet are in contact with the running surface and are well forward under the body. The front feet have left the running surface and are sharply flexed at the wrists with palmar surfaces facing upward. The anterior region of the body is being propelled forward and upward. The patagia have been retracted preventing interference with the action of the limbs. The tail is arched. X 0.47.





PLATE 32

Early bounding phase.

This phase follows immediately after that in Plate 31. Heels have been raised as the hind limbs begin to straighten in order to propel the body forward. The front feet have begun to rotate forward about the wrists. Back and tail are straightening. X 0.47.





PLATE 33

Early bounding phase.

The hind feet from ankle to the base of the toes are now approximately perpendicular to the running surface. Suspension is entirely by the digits of the hind limbs acting in a paired fashion. Front legs have rotated forward to a point at which the paws are almost directly under the shoulders. Palmar surfaces are perpendicular to the long axis of the body. The arch of the back is still further reduced. The body mass has been propelled forward of the point of contact of the hind feet. X 0.47.



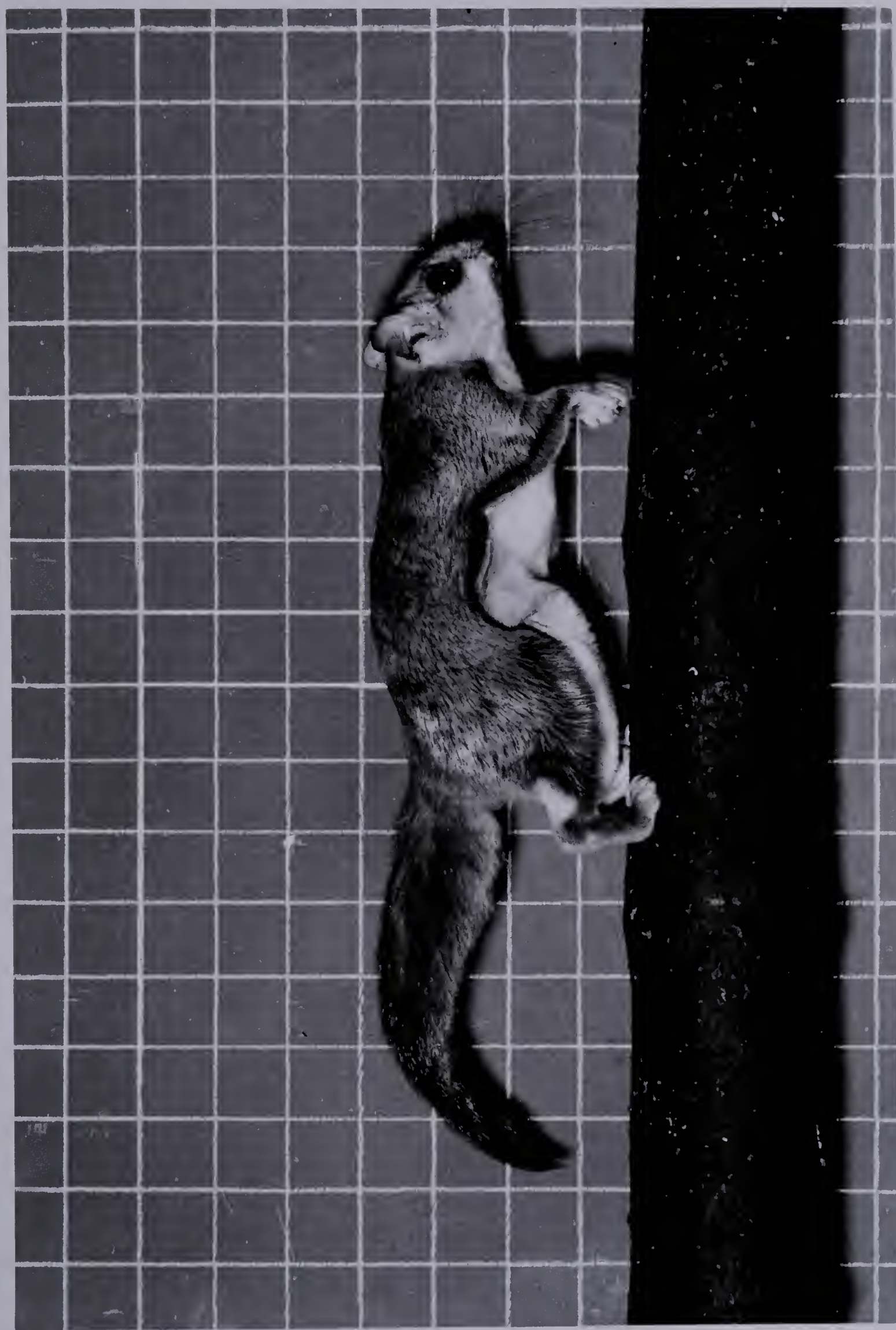




PLATE 34

Early bounding phase.

Back, tail and hind limbs have straightened; the squirrel is about to become airborne. Fore limbs have begun to reach forward the paws continuing their rotation. The long axis of the body is inclined at an angle to the running surface. X 0.47.



PLATE 35

Intermediate bounding phase.

The body is stretched out during the first period of suspension. The hind feet are well to the rear and at near-minimum distance apart with the plantar surfaces rotated inward. The fore feet reach forward under the chin with palmar surfaces downward. The body is approximately in a straight line. There appears to be some tension upon the margin of the patagium. X 0.47.





PLATE 36

Intermediate bounding phase.

The squirrel is about to touch down with the anterior region inclined downward. The head has been slightly raised and the fore feet lowered. Hind feet have begun to swing forward but in this case are not acting quite in unison.

X 0.47.





PLATE 37

Intermediate bounding phase.

The body is tilted quite sharply forward. The left front foot is about to make contact with the running surface somewhat earlier than its right counterpart. The hind legs are swinging forward, accelerating with respect to the body. Plantar surfaces are rotating into a position in line with the landing surface. The back has begun to arch. The completion of this stride would probably exemplify the half-bound in which the hind limbs operate in a paired fashion while one fore foot touches down prior to the other. X 0.47.





PLATE 38

Intermediate bounding phase.

This plate differs from the previous one (Plate 37) in which there was considerable difference in time and space between the contact of one front foot with the running surface and the contact of the other member of the pair. In this plate, both front and hind feet are acting in approximately paired fashion. This is characteristic of the bound. X 0.47.







PLATE 39

Later bounding phase.

Both fore feet have contacted the running surface in close proximity to one another. The body is still inclined forward. Hind feet are moving forward and outward, initiating an arch in the back. The head is slightly raised and the patagia are retracted. Much of the weight of the anterior part of the body is now directly over the front feet. X 0.47.



PLATE 40

Later bounding phase.

Front feet grip the running surface firmly.

The hind feet are rapidly accelerating with respect to the body, moving both forward and outward away from the midline. With the forward motion of the hind limbs, the back continues to arch in the lumbar and sacral regions. The tail streams directly behind.

X 0.47.





PLATE 41

Later bounding phase.

The back continues to arch and an arch has developed in the tail. The fore feet, having pulled the body forward from the position in the preceding plate (Plate 40), are on the point of leaving the running surface before the hind feet have yet made contact. Hind feet are passing well forward and outside the front feet, their plantar surfaces horizontal.

The back is tightly arched. Note the decided arch in the tail. X 0.47.





PLATE 42

Later bounding phase.

All four feet are off the running surface in a second but brief period of suspension. Here, the front feet have left the running surface while the hind feet have not yet made contact. The back is arched to the maximum extent due to the over-reach of the hind limbs. The tail is arched. X 0.64.





PLATE 43

Later bounding phase.

All four feet are still off the running surface during the second period of suspension. The front limbs, with paws flexed sharply at the wrists, are rotating forward and accelerating with respect to both the hind limbs and the body. The hind feet are about to make contact with their plantar surfaces. The back is still arched markedly but the imminent separation of fore and hind limbs will again straighten the spine.

The tail has lost the pronounced arch present in Plates 41 and 42. The undulation of the tail during these running strides probably adds a little momentum and may even assist in supporting the pelvis in the air while the hind limbs are swinging forward. Dogs make use of the tail in a similar fashion while horses often swing the head forward and backward in the line of motion. X 0.47.







PLATE 44

Later bounding phase, quarter rear view.

This phase is very similar to the preceding one (Plate 43), although the hind feet have come to ground, terminating the second period of suspension. Note the very wide spread of the hind feet which have passed forward and around the front feet. Note, too, the plantigrade aspect of the hind feet and the manner in which the palmar surfaces of the front feet tend to assume a position along the ventral surface of the squirrel. X approximately 0.66.





PLATE 45

G. sabrinus laying a scent trail.

Note the arch of the spine and attitude of the tail. The genital region is in close contact with the running surface as the squirrel emits droplets of urine. When introduced to new surroundings, northern flying squirrels tend to deposit such droplets at varying intervals before moving about freely.

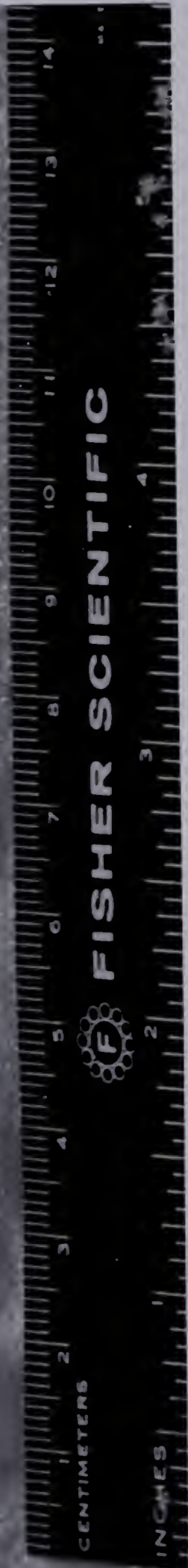




PLATE 46

Tracks associated with the half-bound in Glaucomys sabrinus.

These impressions were made on March 14, 1965 in a thin layer of snow which had been freshly deposited upon an underlying deep layer of heavily crusted snow. The squirrel was travelling from right to left. Note the over-reach of the hind feet and the fact that one front foot (the right) has preceded the other in making contact with the snow while both hind feet have come down at approximately the same time.



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PLATE 47

Change of lead in Glaucomys sabrinus.

These impressions were left in deep soft snow on March 16, 1965. The squirrel was travelling from right to left utilizing the half-bound which, at times, merged into the full bound. This set of tracks immediately preceded that in Plate 48. Note that the right front foot has made contacts slightly before the left front one, while the hind pair have come down almost simultaneously.



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PLATE 48

Change of lead in Glaucomys sabrinus.

These impressions were left in deep soft snow on March 16, 1965. The squirrel was travelling from right to left. This set of tracks followed immediately after those in Plate 47 and illustrates a change of lead with the front feet. Here, the left front foot has slightly preceded the right front member in making contact with the snow. The impression is very close to that made during the full bound in which both front and hind feet function in paired fashion, the front pair making contact with the running surface before the hind pair.



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PLATE 49

Series of strides in G. volans.

The squirrel is bounding at approximately 700 strides per min and a velocity of approximately 6.3 miles per hour.

Subject and grid at 4 ft.

Strobolume at 700 cpm. High intensity.

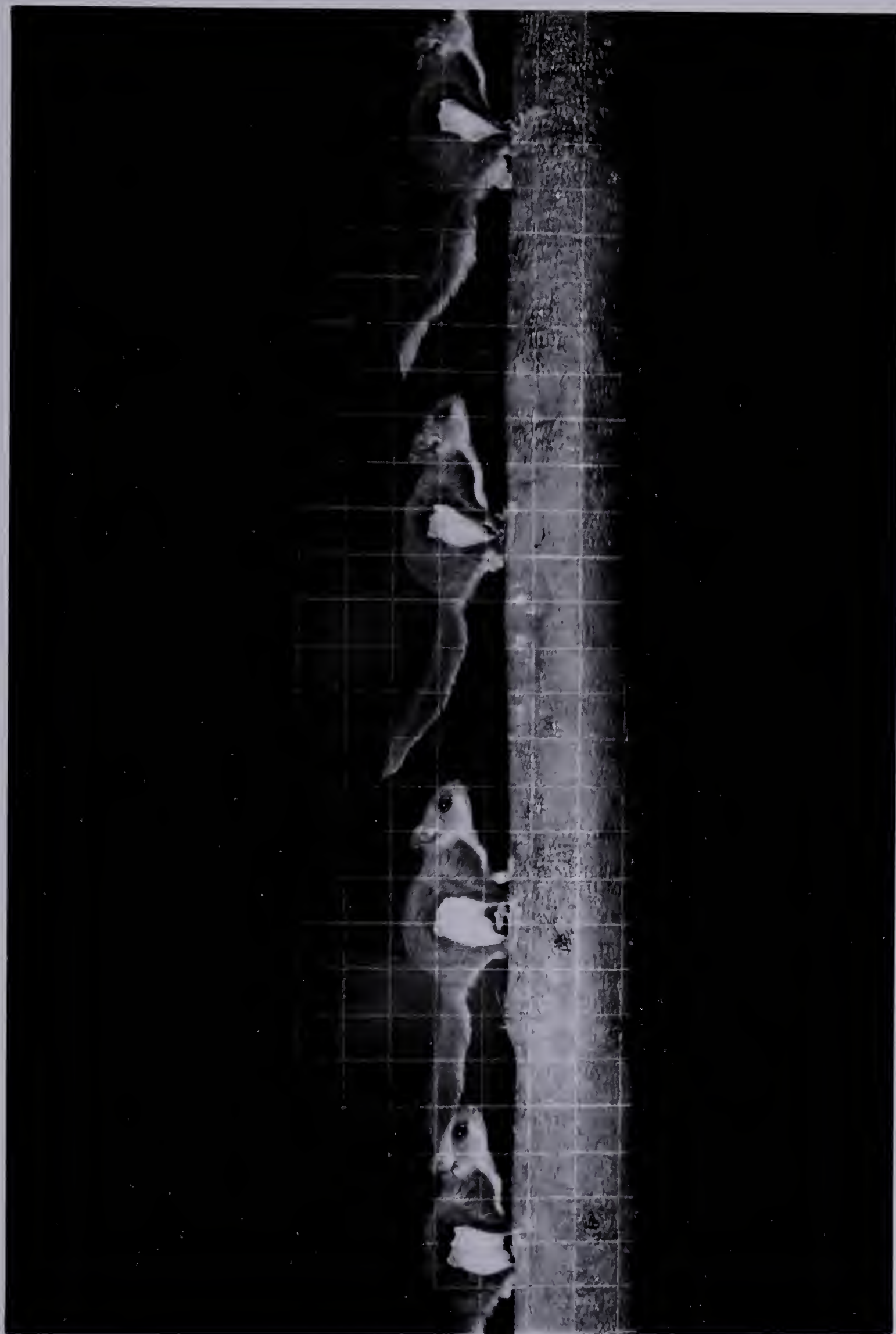




PLATE 50

Early bounding phase in G. volans.

The front feet have been raised from the running surface and swung forward. The plantar surfaces of the hind feet are no longer in complete contact with the log. The spine is markedly arched and the hind limbs are about to exert their thrust upon the running surface. This phase is slightly earlier than that in Plate 31 (G. sabrinus). X 0.66.



PLATE 51

Early bounding phase in G. volans.

The heels are raised higher than in Plate 50 while the front limbs have swung still farther forward. The spine is less arched and the front paws have been flexed about the wrists bringing their palmar surfaces upward. Compare with Plates 31 and 32 (G. sabrinus). X 0.66







PLATE 52

Intermediate bounding phase in G. volans.

The body is stretched out in the first period of total suspension. The hind feet are well to the rear and close together with plantar surfaces facing inward. The front feet reach well forward under the chin with palmar surfaces downward. Compare with

Plate 35 (G. sabrinus). X 0.69

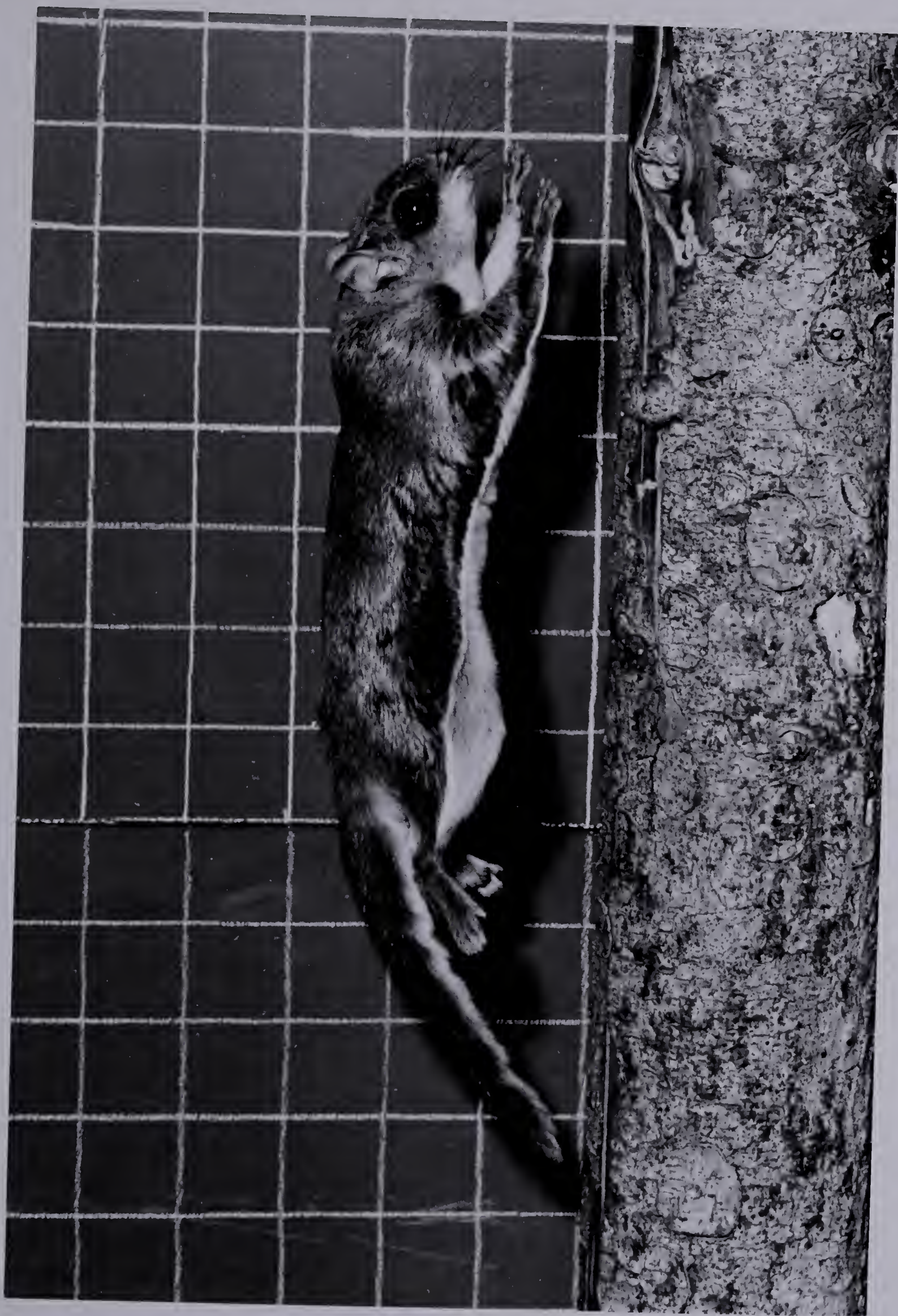


PLATE 53

Intermediate bounding phase in G. volans.

The right fore paw is about to touch down and will be followed shortly by the left member of the pair. The hind feet are swinging forward, accelerating with respect to the body.

Compare with Plate 37 (G. sabrinus).

X 0.70.



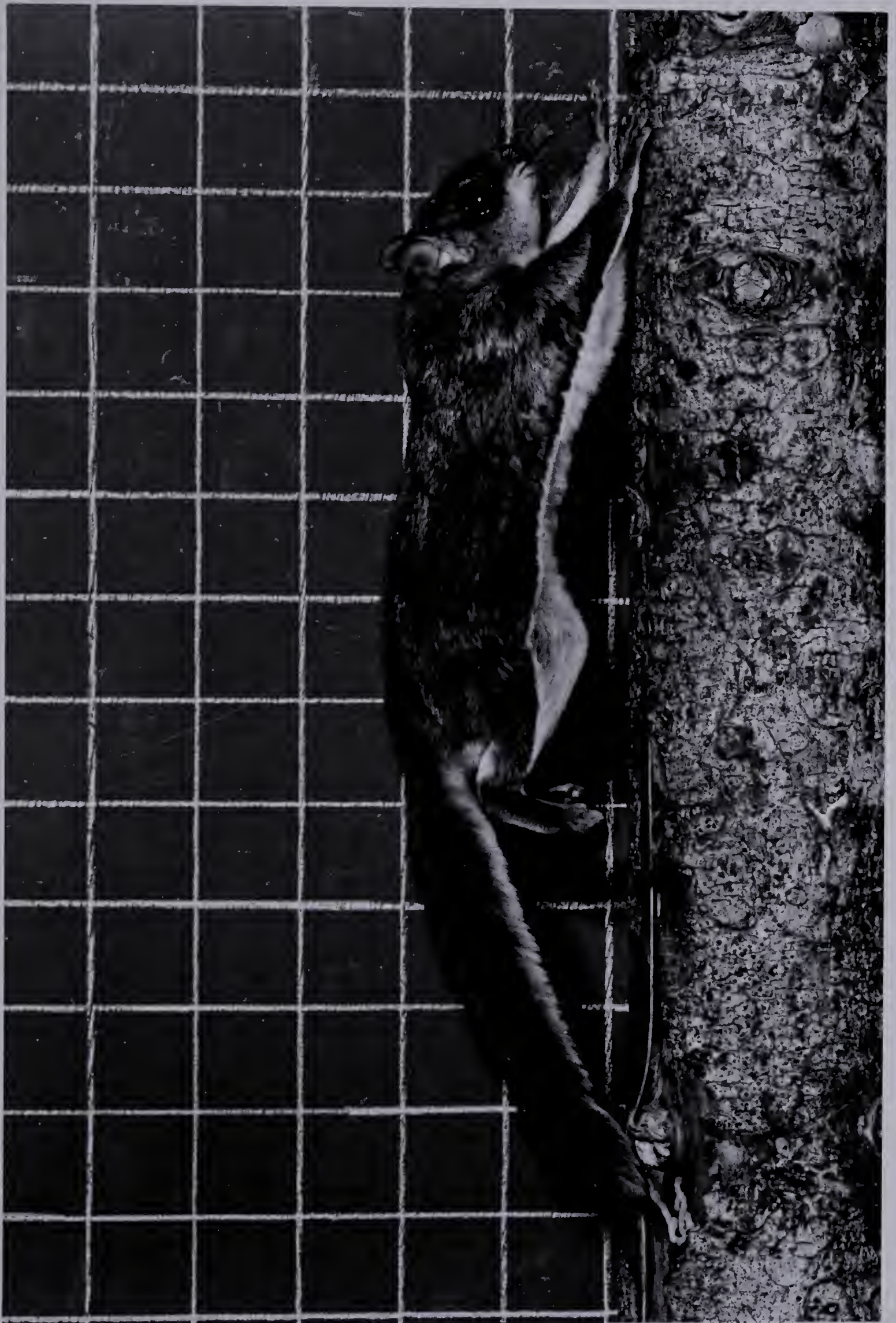




PLATE 54

Intermediate bounding phase in G. volans.

The body is inclined forward to the running surface as the front feet are about to make contact. Already the hind limbs have begun to swing forward, arching the spine. Compare with

Plate 37 (G. sabrinus). X 0.70



PLATE 55

Later bounding phase in G. volans.

Both front feet have made firm contact with the running surface. The body is inclined forward. The hind feet are moving both forward and apart in order to pass around the front limbs. The spine is decidedly arched. Compare with Plate 39 (G. sabrinus). X 0.66







PLATE 56

Later bounding phase in G. volans.

The hind limbs are rapidly accelerating with respect to the rest of the body. The arch of the back is more pronounced. Compare with Plate 40 (G. sabrinus). X 0.70



PLATE 57

Later bounding phase in G. volans.

The hind feet are about to pass forward around the front feet which are still in firm contact with the

log. Compare with Plate 41 (G.

sabrinus). X 0.67







PLATE 58

Bounding phase in G. volans while carrying nut.

This is a characteristic carrying attitude in this species. Fine cavities are first made in the end of the nut allowing a firm grip with the incisors. Then the nut is picked up and transported in the manner illustrated. All limbs are thus freed for locomotor activity. Nor does the additional weight at the extreme anterior end appear to interfere appreciably with gliding and parachuting activity. Northern flying squirrels also carry food items in this manner. X 0.64





## VII. PROGRESSION UPON VERTICAL SURFACES

Northern flying squirrels are well adapted for progression in almost any direction upon vertical surfaces so long as the substrate affords them an effective grip. The feet are equipped with extensive fatty pads as well as the terminal claws on the digits (Plates 28 and 59).

### The Ascent

Rapid ascent of tree-trunks is accomplished by means of a footfall pattern in which fore limbs and hind limbs move in pairs. This gait is similar to the bound characteristic of the species when running except that there is no over-reach of the hind limbs and no period of total suspension. Hind feet grip the tree firmly as the front feet are advanced, and vice versa. It is interesting to note in this connection that the spread of the front and hind pairs of limbs (Plate 60) is the reverse of the pattern used during bounding progression upon horizontal surfaces (Plate 44). On narrow tree-trunks, the palmar surfaces of the front feet oppose one another on either side of the tree while the plantar surfaces of the hind feet are placed side by side and at right angles to the plane of the soles of the front feet. All of these aspects are clearly illustrated in the accompanying motion picture film.

Slow ascents may be accomplished by means of the diagonal walk.





### The Descent

Descent of tree-trunks by northern flying squirrels is more complex and more varied. When descending slowly the tendency is to maintain firm contact with the tree by advancing only one foot at a time while clinging with the other three feet. However, the time intervals between footfalls are unequal and there is a marked tendency for both front and hind pair to move as closely spaced couplets with a relatively longer period of time intervening between movement of the last fore foot of the pair and the movement of the succeeding hind foot. Another pause may ensue before the front feet are again advanced.

At times there appears to be some reluctance on the part of the squirrel to let go with the last hind foot. At such times, the animals may pause for several seconds with a single hind foot extended well behind gripping the bark securely (Plate 61). They frequently pause with both hind limbs extended well to the rear and may even feed while clinging, head downward, in this fashion. So supported, the front feet are free for food handling. Throughout slow descents the ventral surface of the squirrel is closely appressed to the tree-trunk while the aspect of the digits suggests that a substantial component of the force exerted by the limb while clinging to the trunk is directed inward towards the midline of the body (Plate 61).

Rapid descent is accomplished somewhat after the fashion of rapid ascent except that both front and hind pair of limbs are broadly



spread. If the tree is slender, the plantar surfaces of the hind feet tend to oppose one another in clasping fashion as the front feet are advanced. There is no period of total suspension here since at least one pair of limbs is in contact with the tree at all times.

Often the last two or three feet of descent is accomplished by means of gliding or parachuting. In such cases the half-bound is utilized just prior to take-off, the fore feet shifting during the last running stride so that one fore foot makes contact well before the other. All of these details are illustrated in the accompanying motion picture film.



PLATE 59

Left hind foot of G. sabrinus. Ventral view.

The foot is well equipped with fatty pads and the digits terminate in stout sharp claws which in this plate are partially obscured by the long winter pelage.



PLATE 60

G. sabrinus ascending a broad vertical surface.

The paired front feet are widely spread, while the hind pair are placed close together under the body. This relationship of front and hind feet is the reverse of that characteristic of the bounding gait of the species upon horizontal surfaces.



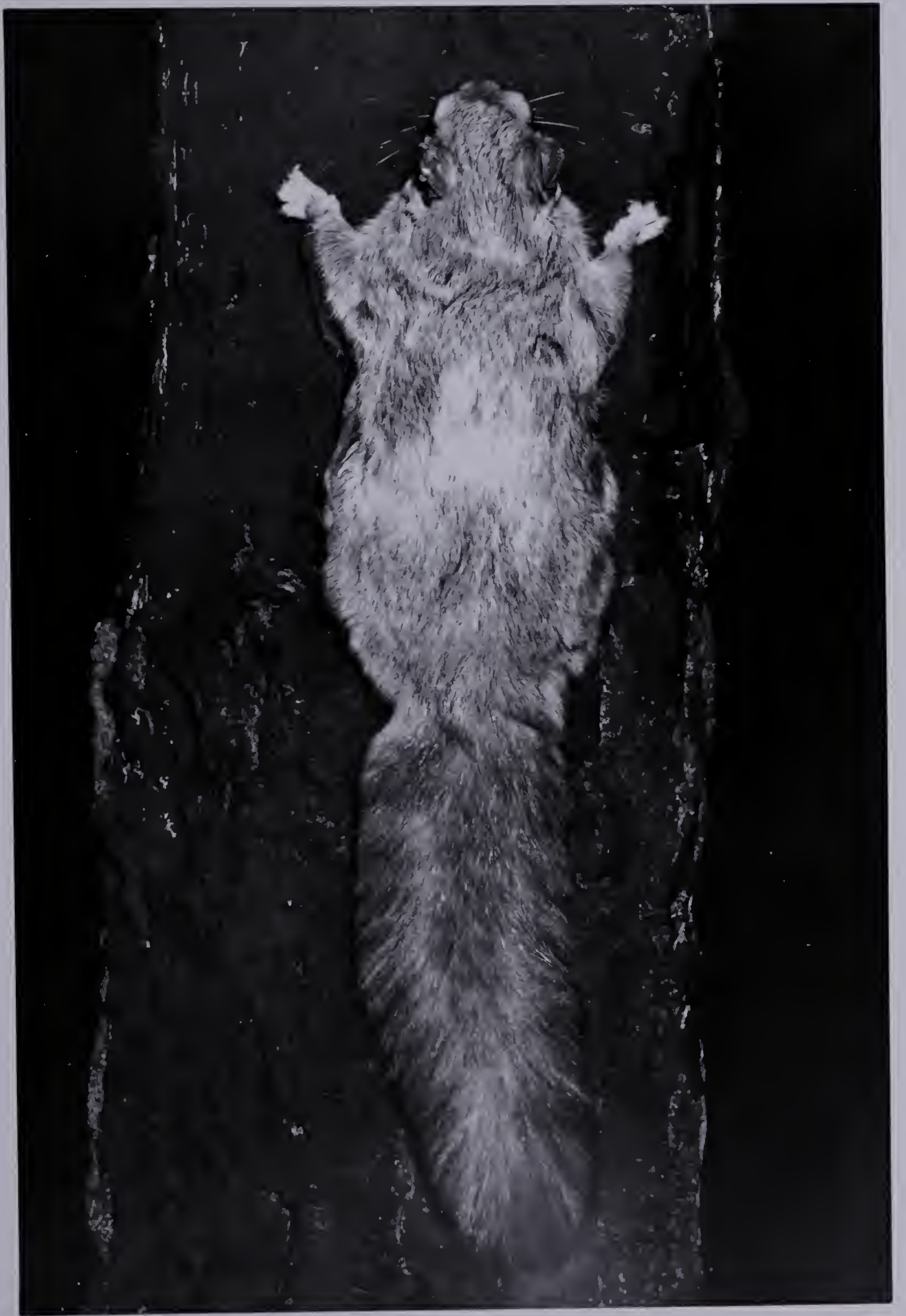




PLATE 61

G. sabrinus descending a broad vertical surface.

The subject is descending slowly, moving a single foot at a time. The ventral surface of the squirrel is closely appressed to the tree-trunk. Note the manner in which the claws of the right hind foot are hooked to the surface and the fact that a component of the effort appears to be directed inward towards the long axis of the body.





## VIII. PROGRESSION THROUGH THE AIR

### Trajectory

The trajectory of the northern flying squirrel varies with the distance travelled. On very short glides there is little loss of height since the squirrel is able to launch with considerable force acting in a forward and upward direction. Even so, the trajectory is a curve with the animal rising to a maximum height and then gradually falling off as the target is approached (Plate 62).

Longer glides are usually characterized by a brief initial phase in which the squirrel gains altitude from the muscular effort exerted during launching. This is followed by a short transitional phase in which the animal levels off before beginning the descent. The descent varies a good deal and may be characterized by either gliding or parachuting as defined by Oliver (1951). Also, there is a tendency for an early gliding phase to be followed by a parachuting phase which, in turn, may be followed by a second gliding or planing phase after the animal has gained sufficient momentum.

Fig. 11 includes a number of successive points recorded for each of 12 short trajectories as well as the completed curve from launching to landing for one of these. When vertical distance ( $S$ ) is plotted against time ( $t$ ) squared, the resulting curve deviates little from a straight line, indicating the essentially parabolic nature of the trajectory represented by this curve. When the





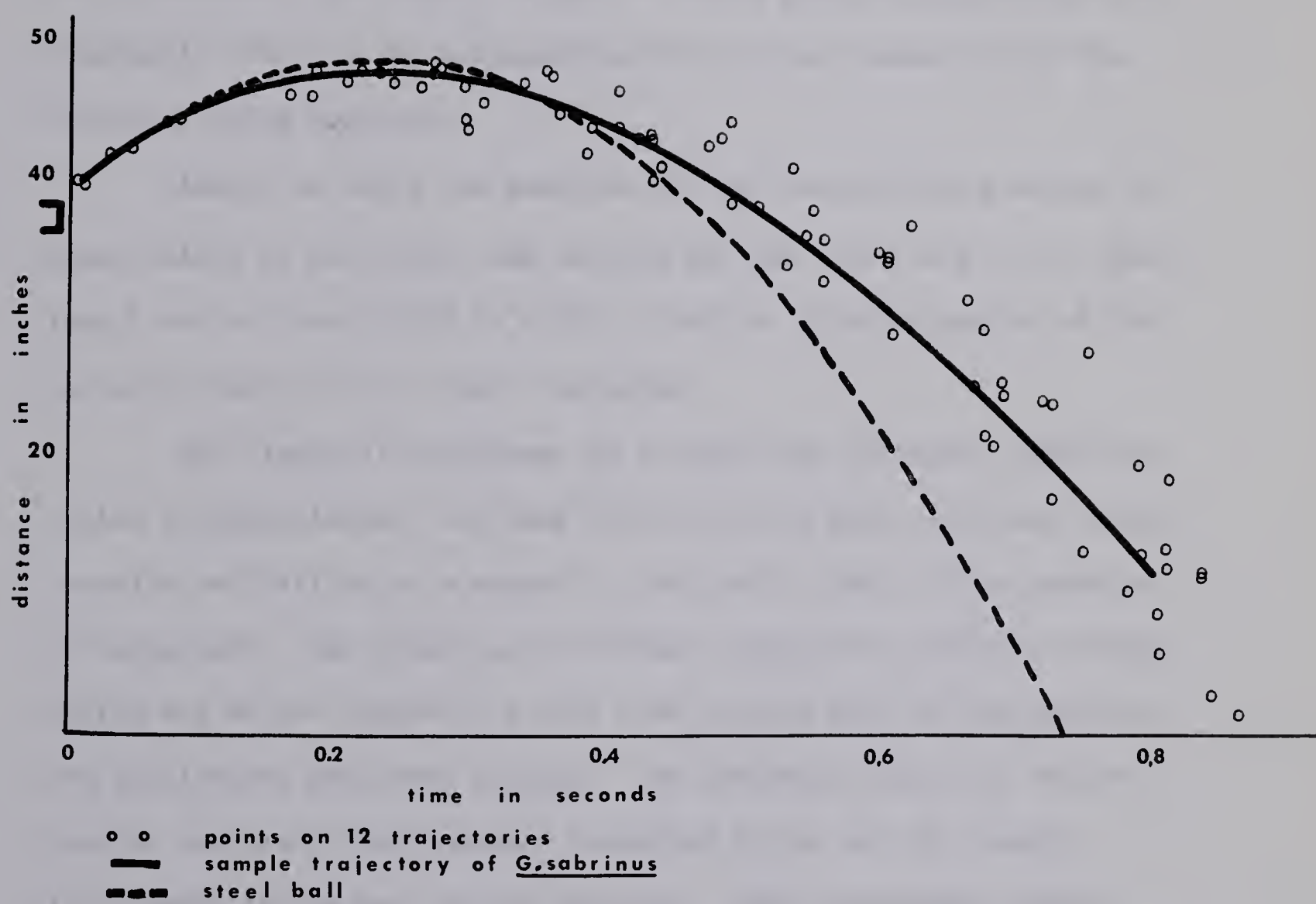


FIG 11 Trajectories of northern flying squirrel and steel ball.



coordinates of the well-defined eye of the squirrel in successive positions are substituted in the general quadratic equation and the values of a, b and c determined, the equation for this curve is  $S = -100t^2 + 30t + 28$ . It is important to note that the trajectory does not fit this equation exactly throughout; the subject is neither inanimate nor passive but is continually making physical adjustments as it descends. The nature of many of these physical adjustments is abundantly clear in the accompanying film on the locomotion of the northern flying squirrel.

Again, on using the equation  $Y = kx^2$ , substituting values for known points on the curve, and solving for the value of k, it is found that k varies from 0.0139 to 0.0143. This is also indicative of the parabolic nature of the short trajectory.

The classical trajectory of a steel ball (Littler, 1949) projected in approximately the same direction with about the same initial velocity and falling in a vacuum is included in Fig. 11 for purposes of comparison. The steel ball continues rising for a slightly longer period but on the descent its path soon crosses that of the squirrel and accelerates much more rapidly. The retarding effect of the extensive surface of the squirrel presented to the air is clearly illustrated in the path of the squirrel. This retardatory effect profoundly influences landing velocities. For example, the descending landing velocity of the squirrel whose trajectory is represented was approximately 130 inches per sec after a glide of 0.8 sec duration.





Had this animal been launched in a vacuum under similar conditions, its velocity at the same point in time would have been approximately 277.2 inches per sec.

The first derivative of the equation for the squirrel's descent gives a velocity of  $(-200t + 30)$  inches per sec as opposed to  $(-384t + 30)$  for the steel ball. The respective second derivatives give an acceleration of -200 inches per sec per sec for the squirrel's trajectory as opposed to -384 inches per sec per sec for the steel ball. It would appear that the lift of the squirrel is approximately equal to half its weight (J.M. Smith pers. comm., 1965).

It is realized that the foregoing material regarding trajectories has definite limitations and that the analysis is in some respects unsatisfactory. The trajectories plotted are short ones and the squirrels have had little time to gain momentum. The curve fits the derived equation better at intermediate points than it does at either end. At least part of this is due to the fact that the point of reference (the squirrel's eye) is situated at some distance from the centre of gravity of the animal and tends to rotate about this point as the squirrel changes attitude on launching and landing. As stated earlier, the subjects are constantly making physical adjustments which influence their course as they descend; it would be highly unlikely that acceleration would remain near-constant for any appreciable portion of the trajectory.



It was not possible to learn much about the gliding efficiency of northern flying squirrels during long descents by studying them in the indoor laboratory since space was too limited. However, an excellent opportunity to record the efficiency of a single individual was afforded by a wild squirrel which came to our bird feeding station by the window on many nights during the winter of 1964-65. The feeding station was attached to a bare spruce pole which had been wired to the eaves of the house for support. After having fed, the squirrel often climbed to the top of the pole supporting the feeder and then sailed off in the direction of a power pole illuminated by the yard light. Following fresh snowfalls, it was possible to record his landing points in the snow near the base of the pole, apply a carpenter's level, and compute the pertinent data. Six such glides covered horizontal distances of 38.7, 39.3, 41.5, 40.8, 40.5 and 41.9 ft respectively. The mean horizontal distance covered was 40.5 ft per glide, during which the animal lost 13.75 ft in altitude. The mean ratio of horizontal distance covered to loss of altitude in these instances was 40.5 : 13.75 or 100 : 34. The squirrel lost approximately 1 ft in 3.

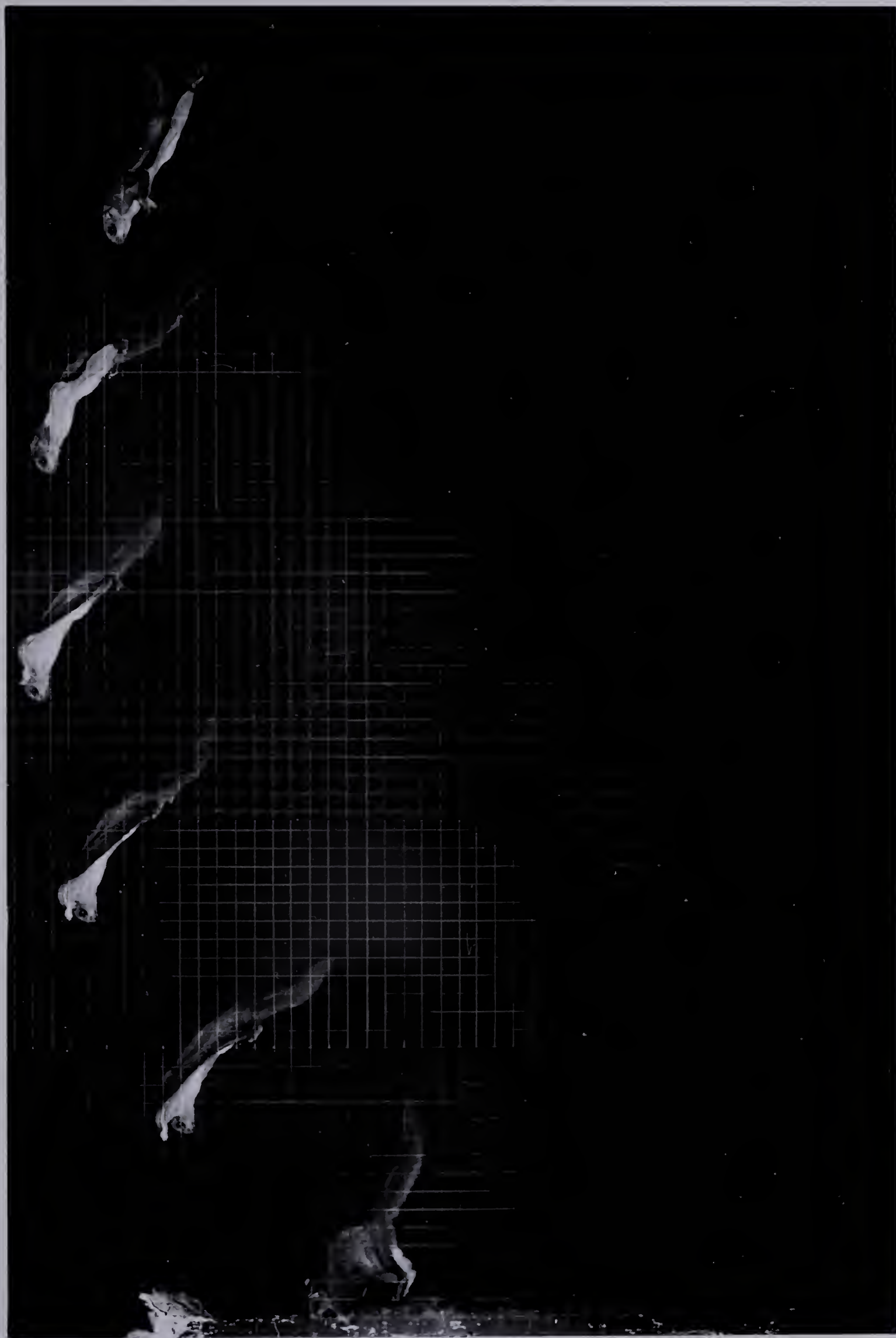


PLATE 62Trajectory of Glaucomys Sabrinus.

Launching was accomplished by a running take-off. The squirrel gradually swings into a braking position prior to landing. The equation for the trajectory is approximately  $S = -100t^2 + 40t + 13$  giving an initial velocity of about 40 in per sec and a landing velocity of approximately 80 in per sec. Acceleration is approximately -200 in per sec per sec.

Subject and grid at 10 ft.

Strobolume at 600 cpm. High intensity.





### Gliding and Parachuting

Much has already been said about the characteristic gliding attitude of northern flying squirrels. Plate 27 will serve to illustrate the ventral view while Plates 63 and 64 show various stages of both gliding and parachuting. With respect to these activities, the definitions of Oliver (1951) have been adopted in this paper. Thus parachuting can be considered as the making of a retarded descent along a path that deviates from the vertical by not more than  $45^{\circ}$ , whereas gliding is the performing of a retarded descent along a path of more than  $45^{\circ}$  from the vertical. Naturally these modes of descent will merge from one to the other.

Plate 27 clearly illustrates at least part of the function of the cartilaginous rod attached to the pisiform. When abducted this rod increases tension upon the patagium and at the same time provides additional more or less rigid support in the anterior region of the membrane. This plate clearly shows the pronounced fold of skin at the anterior margin of the patagium extending from the side of the neck almost to the wrist. There can be little doubt that this fold assists the functioning of the patagium as an aerofoil. As in the wings of birds (Storer 1948), the leading edge is relatively rigid while the trailing edge tends to be more flexible.

Plate 63 illustrates that during both parachuting and gliding the head is lowered. The dorsal surface tends to be somewhat convex while the ventral surface exhibits some degree of concavity. The





relative position of the limbs is undoubtedly important in contributing stability. Oliver (1951), reporting on parachuting amphibians and reptiles, observed that such forms tend to assume similar attitudes when descending. Sellick (1960) pointed out that in skydiving the most stable attitude involves spreading the arms and legs to their maximum extent and holding them higher than the trunk. The Frontispiece illustrates a similar gliding attitude in northern flying squirrels.

The broad flat tail at the rear most certainly serves as a stabilizer with regard to controlling pitch, while the patagia are free to serve in a somewhat similar capacity in the control of roll. It appears that yaw is probably controlled by either the tail or relative limb position, or both. Skydivers (Sellick 1960) are able to rotate at will merely by slightly raising or lowering a single limb.

By definition, parachuting is associated with steeper descents. The next to last images in Plates 63 and 64 illustrate this phase. The general attitude of the body is horizontal. The head is slightly raised and the limbs moderately lowered. At the same time, tension upon the patagia is maintained resulting in greater concavity of the ventral surface. The tail extends directly behind presenting maximum surface to the air.

When observing northern flying squirrels in the wild, steep trajectories were often noted in which the majority of the descent consisted of parachuting. However, these trajectories usually terminated in a brief gliding or soaring phase during which the animal



braked, checking forward speed. Still other long glides were characterized first by a short gliding phase, next a parachuting phase in which the subject visibly picked up speed, then a gliding phase with much horizontal displacement and finally, still another parachuting phase. Here, gliding and parachuting appeared to merge smoothly into one another.

Northern flying squirrels tend to use their patagia even when losses in altitude are slight and their use would seem unnecessary. The determining factor appears to be a sufficiently long period of suspension to allow them to spread the limbs and patagia and return the limbs once again to landing position under the body. It was found experimentally that if an individual were provided with a launching surface such as a rough board which afforded a secure grip, the squirrel would launch itself and spread the patagia fully for altitudes exceeding 2.25 in above the floor. However, when a smooth metal surface was substituted for the rough board the animal did not utilize its patagia until the altitude above the landing surface reached 12.25 in. Twelve successive leaps from the relatively rough launching surface placed at an altitude of 6 in above the horizontal landing surface ranged from 29.75 to 33.50 in. in length with a mean distance of 31.92 in. All involved fully spread patagia. Probably 29.75 in, if converted to time, was close to the minimum period of transit permitting extension and retraction of the limbs and patagia for this individual.



PLATE 63

Gliding and parachuting trajectory of G. sabrinus.

Launching was from a standing take-off.

The squirrel maintains a relatively horizontal attitude for braking and stability during the relatively long parachuting phase.

Subject and grid at 10 ft.

Strobolume at 600 cpm. High intensity.



PLATE 64

Gliding and parachuting trajectory of G. sabrinus.

Launching was from a standing take-off.

Gliding merges into parachuting during the last tenth of a second before landing.

Subject and grid at 10 ft.

Strobolume at 600 cpm. High intensity.







### Launching

Launching (Plates 65 and 66) is preceded by head-bobbing which appears to be associated with gauging distance to target. Immediately prior to launching from a horizontal surface, the squirrel shuffles into a position with hind limbs advanced as far as possible and plantar surfaces firmly gripping the take-off surface. Front paws are usually placed close together with hind paws more lateral and the back is markedly arched. The squirrel then draws itself back as far as possible without loosening its grip, as though to fully cock the propelling muscles of both front and hind limbs. This phase is particularly well illustrated in the motion picture sequence included in the study. The actual launching is usually forward and upward in direction and is precipitated by the pull of the fore limbs together with the powerful thrust of the hind limbs. In this action, the hind limbs swing through an angle of approximately  $135^{\circ}$  and trail directly behind for 0.1 - 0.2 sec after the animal becomes airborne. The tail, initially cocked, snaps sharply into line possibly adding a little to the impetus.

If the glide is a short one (Plate 66), the back is arched almost immediately and the legs brought into landing position with the posterior part of the body approximately vertical. However, this is only true if the squirrel is about to land upon a vertical surface. Should the glide be a longer one, the squirrel quickly assumes the characteristic gliding attitude with the limbs fully spread and the



patagia taut (Plate 63). Landing upon horizontal surfaces is dealt with in the next section.

Plate 67, taken from directly below, illustrates the early stages of take-off from the ventral view. In the first image, the body is reaching forward with the hind limbs straightening simultaneously. The abdominal region is constricted with the margins of the patagia in that area meeting mid-ventrally. The fore limbs, flexed at the wrists, are rotating forward and outward in order to provide support for the patagia.

In the second image the fore limbs have assumed gliding position with the patagia stretched tautly from carpals to the base of the head. The front paws have rotated vertically with palmar surfaces outward and digit V upward. The cartilaginous rods are beginning to come into play, contributing added tension to the patagia. Hind legs are swinging forward into gliding position with paws turned sharply outward. The fourth image illustrates characteristic stable gliding attitude.

The squirrels are also able to launch themselves backward from an upright, vertical position on a tree trunk. In such cases, they appear to exert greater force with one lateral pair of limbs than the other which causes the body to spin for  $180^{\circ}$  about its long axis. Gliding position is then quickly assumed. On occasion, an individual was noted executing a complete back roll from a vertical position on a tree trunk to land lower down in the original position. The manoeuvre was too infrequent and complex to analyze in any detail. The accompanying film illustrates a number of variations of these manoeuvres.



PLATE 65

Launching from a horizontal surface.

The initial image is blurred because of successive exposures while the subject bobs prior to take-off. Note the manner in which the tail snaps into line and the patagia are spread in preparation for the 4 ft glide.

Subject at 4 ft.

Strobolume at 600 cpm. High intensity.



PLATE 66

Launching from a horizontal surface.

Since the vertical landing surface is only 30 in from the point of take-off, the body almost immediately assumes landing attitude.

Subject at 4 ft.

Strobolume at 1200 cpm. High intensity.





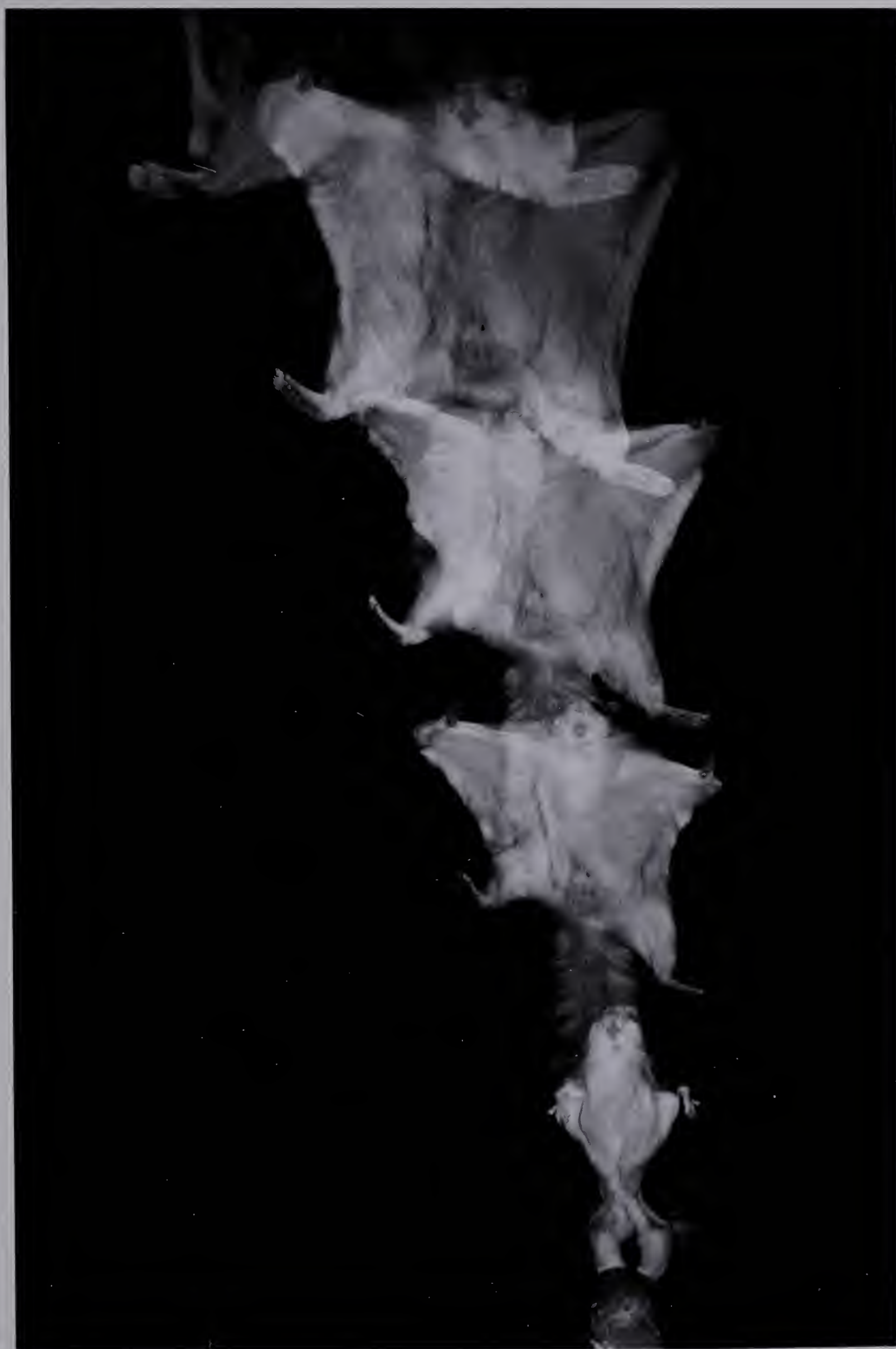
PLATE 67

Launching sequence viewed from below.

The subject is shown from the moment of take-off until full gliding attitude is assumed.

Subject at approximately 5 ft.

Strobolume at 600 cpm. High intensity. Horizontal distance from take-off to vertical landing surface, 6 ft.





### Landing

Landing upon horizontal surfaces varies a good deal from landing upon vertical surfaces although in both cases this manoeuvre tends to be preceded by braking whenever sufficient distance is covered to involve spreading the patagia. In relatively short jumps as in Plate 66, the limbs assume landing position almost immediately after take-off.

Plates 68A to 71 illustrate various phases of landing upon horizontal surfaces at the termination of periods of parachuting. As the squirrel approaches target both fore and hind limbs accelerate with respect to the body, moving forward and under pectoral and pelvic girdles respectively. The paired legs then reach as far forward as possible in order to absorb the shock of landing. The extreme gathering of the hind limbs under the body arches the back in the lumbar and sacral regions. The patagia are retracted by their associated musculature which, according to Grasse' (1955) consists of the carpotarsalis dorsally and the coracopatagialis, patagialis ventralis and dorsopatagialis or humeropatagialis ventrally. The tail is usually held approximately in line with the body while the eyes may be partially or totally closed just prior to contact (Plate 68A).

When landing upon horizontal surfaces contact is usually made first with the hind paws, the front members following shortly. Plate 68A, taken from slightly below, illustrates the relative positions of the feet particularly well. Both members of fore and hind pairs tend





to move in unison as in the bounding gait. Hind feet are brought close together, side by side, with toes well spread and broad plantar surfaces horizontal. The fore paws which had assumed a vertical position for gliding, with palms outward and digit V upward (Frontispiece), have now moved to take up a horizontal position. This initial shift is a very direct one involving only the lowering of the fore limbs without requiring any rotation of the wrists or fore paws. At this point, the elbows begin to swing inward and the fore paws outward, bringing the palmar surfaces into line with the body. The eyes are completely closed; the vibrissae point downwards. In Plate 70 the major shock of landing appears to be borne by the hind limbs.

Landing after a period of gliding is very similar to landing from a parachuting phase. The details are approximately as in Plate 70 in which the portion of the trajectory represented is intermediate between parachuting and gliding. The main difference consists of the braking during which the squirrel assumes a more vertical position, at right angles to the path of motion.

Plate 69 shows that the patagia tend to be drawn somewhat downward at the time of contact because of the extreme reach of the limbs. A limited wild population of northern flying squirrels in the vicinity of the study area provided an opportunity to record tracks of the species in varying snow conditions during the winter of 1964-65. Plate 72 shows two "sitzmarks" of northern flying squirrels landing in deep fresh snow, having glided from an elevation of



approximately 16 ft. Both were travelling from left to right, the tail leaving an impression at the rear. The impressions were made on successive nights. The squirrel registering the imprint in the foreground appears to have been somewhat spread at the moment of impact and did not cut in so deeply.

Plate 73 was secured under somewhat different conditions. The snow had become heavily encrusted after a brief thaw which in turn had been followed by a light snowfall, covering the underlying layers with approximately 0.25 in of fresh snow. The squirrel had glided in from the right and landed on paired feet placed approximately as when landing upon a horizontal log. Faint impressions of the patagia are apparent at the sides. The first stride after landing was a short one characterized by the placement of the hind feet in the tracks left by the front feet. While such strides are common in the genus Mustela, they are very unusual in the northern flying squirrels.

Landing upon a vertical surface tends to vary according to the nature of the activity which precedes landing. If the squirrel has been parachuting as in Plates 63 and 64, the body tends to maintain an approximately horizontal position until the moment of contact with the landing surface. Contact is first made with the outstretched fore limbs while the hind limbs move downward and forward, arching the back. The tail is directly behind until the moment of contact; the head tends to be thrown upward and backward. It seems obvious that





were the squirrel to assume a vertical position while parachuting, he would forego much of the retarding effect conferred by the broad surfaces of the patagia presented at an angle approximately perpendicular to the line of flight.

However, if the squirrel has been gliding immediately prior to landing as in Plates 68, 74 and 62, the body tends to be brought into a more vertical attitude for touching down. It is to be noted that though this tendency exists, the body is rarely quite at right angles to the path of motion. The anterior region of the body is slightly advanced to this plane and the posterior region slightly retarded, presumably to take advantage of the lift provided by the airflow over the surfaces of the patagia. Plate 74 clarifies the successive stages. The body, originally somewhat horizontal in attitude, becomes increasingly vertical as target is approached. Limbs are swung into the forward paired positions, the hind pair taking up a position well under the body thus arching the back. Contact is again first made with the fore paws, the hind pair following very shortly. The head is thrown upward and backward. In Plate 74 the cartilaginous rod can be clearly seen in action.

PLATE 68

G. sabrinus prior to landing upon a vertical surface from gliding phase.

The subject is gliding in from the left. The body has been manoeuvred into an upright position. Fore and hind limbs are about to swing under the body.

Photograph at 1/5000 sec with Dormitzer Syncron electronic flash unit.





PLATE 68A

G. sabrinus landing upon a horizontal surface.

Quarter view.

The squirrel has been parachuting and is coming in for a landing on the top of a stump. The paired limbs are well advanced to absorb the shock. Plantar and palmar surfaces face downward. Hind toes are well spread and the eyes are closed.

Subject at 3.5 ft and slightly above camera level.

Photograph at 1/5000 sec with Dormitzer Synctron electronic flash unit.



PLATE 69

Landing upon a horizontal surface. Side view.

The subject is parachuting in sharply after taking off from a point 4 ft above the landing surface. The broad ventral surface of the body is approximately perpendicular to the line of travel. The patagia are drawn well down as the limbs accelerate with respect to the body.

Subject and grid at 4 ft.

Strobolume at 1200 cpm. High intensity.



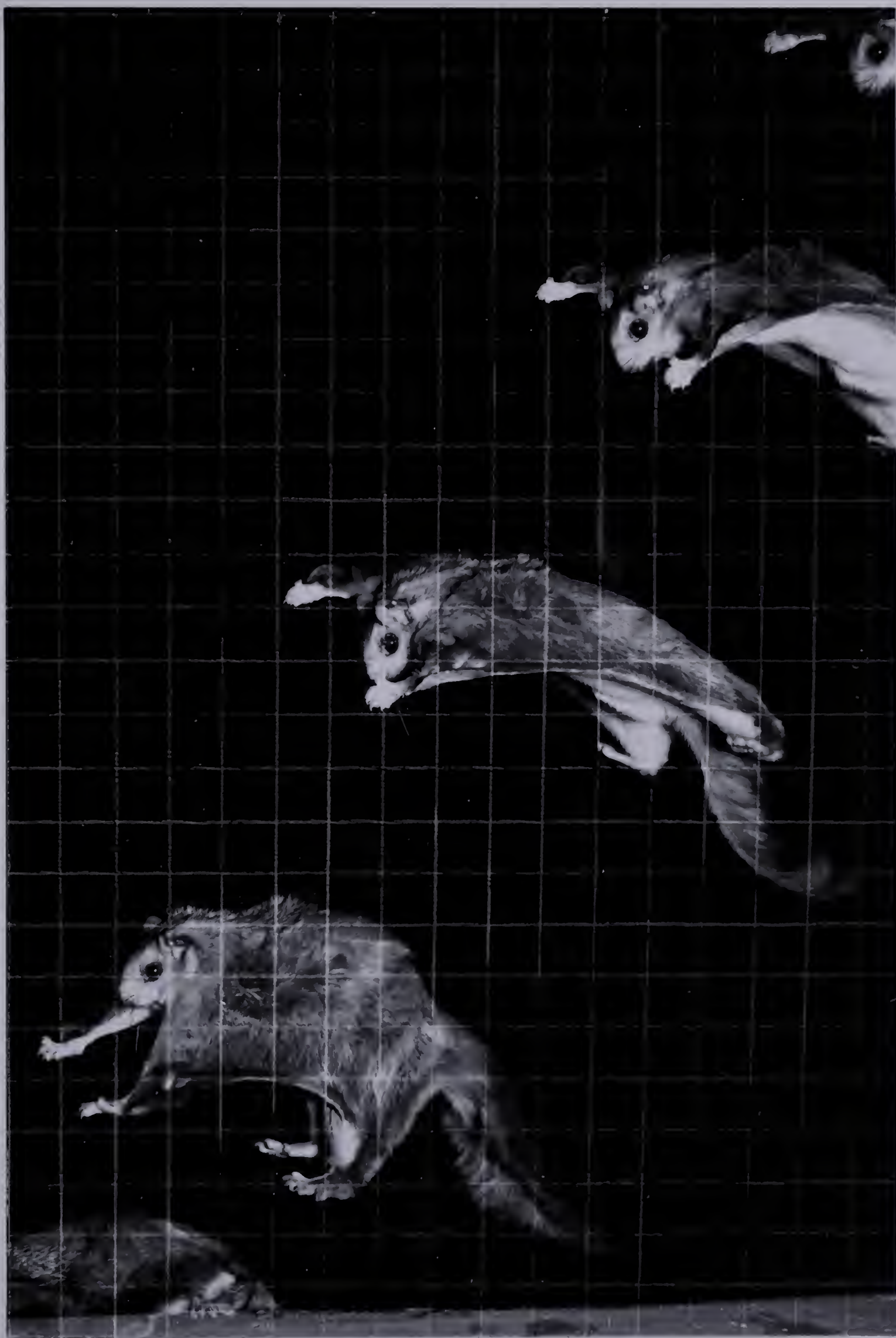




PLATE 70

Landing upon a horizontal surface. Side view.

The squirrel has been travelling in a phase intermediate between gliding and parachuting. The attitude of the body is more perpendicular than in Plate 71 in which the animal is parachuting sharply. Here again, the broad ventral surface is approximately perpendicular to the line of travel. It appears that the major shock of landing is borne by the hind limbs.

Subject and grid at 4 ft.

Strobolume at 1200 cpm. High intensity.

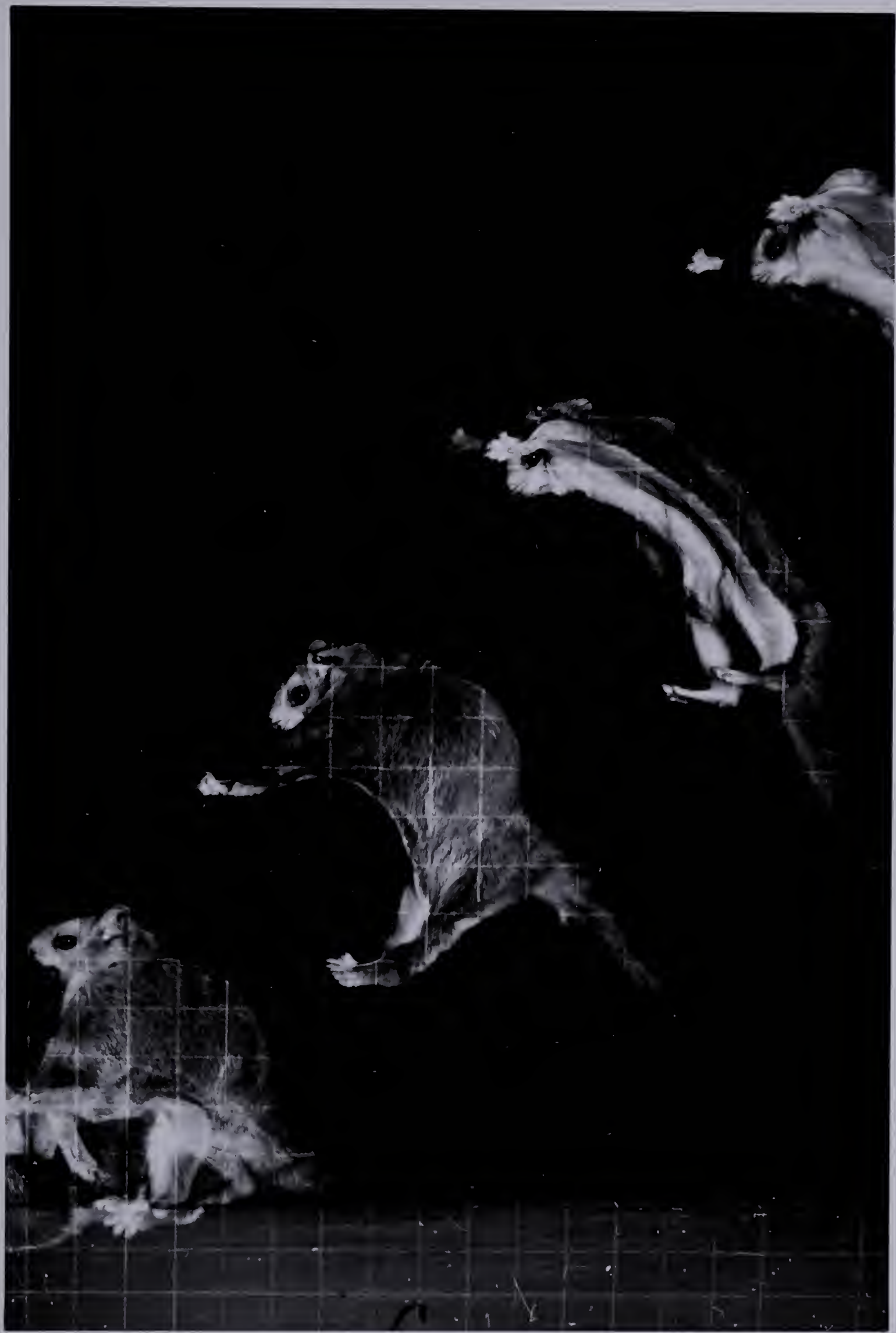


PLATE 71

Landing upon a horizontal surface. Side view.

The hind feet are drawn together under the body with plantar surfaces downward well before the fore feet assume a similar position. The subject is parachuting in sharply. Take-off point was distant 6 ft horizontally and 4 ft vertically from landing point. Compare with Plate 70 in which loss of altitude was 2 ft in a horizontal distance of 5 ft.

Subject and grid at 4 ft.

Strobolume at 1200 cpm. High intensity.

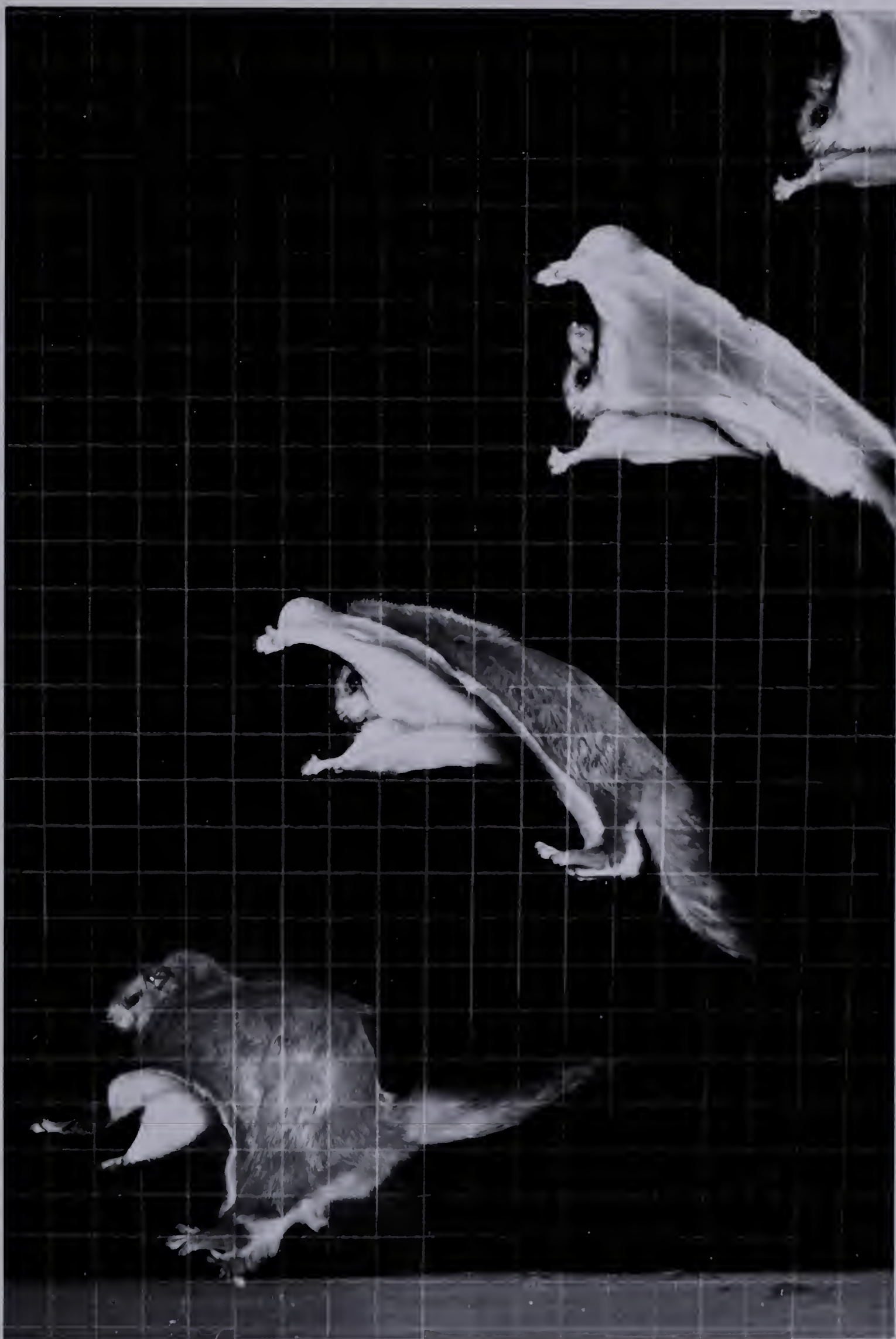




PLATE 72

"Sitzmarks" in deep snow.

These impressions were made on Dec. 9 and 10, 1964 after launching from an altitude of approximately 16 ft. The squirrel was travelling from left to right. Note more pronounced spread of patagia in connection with the image in the foreground.

X 0.35



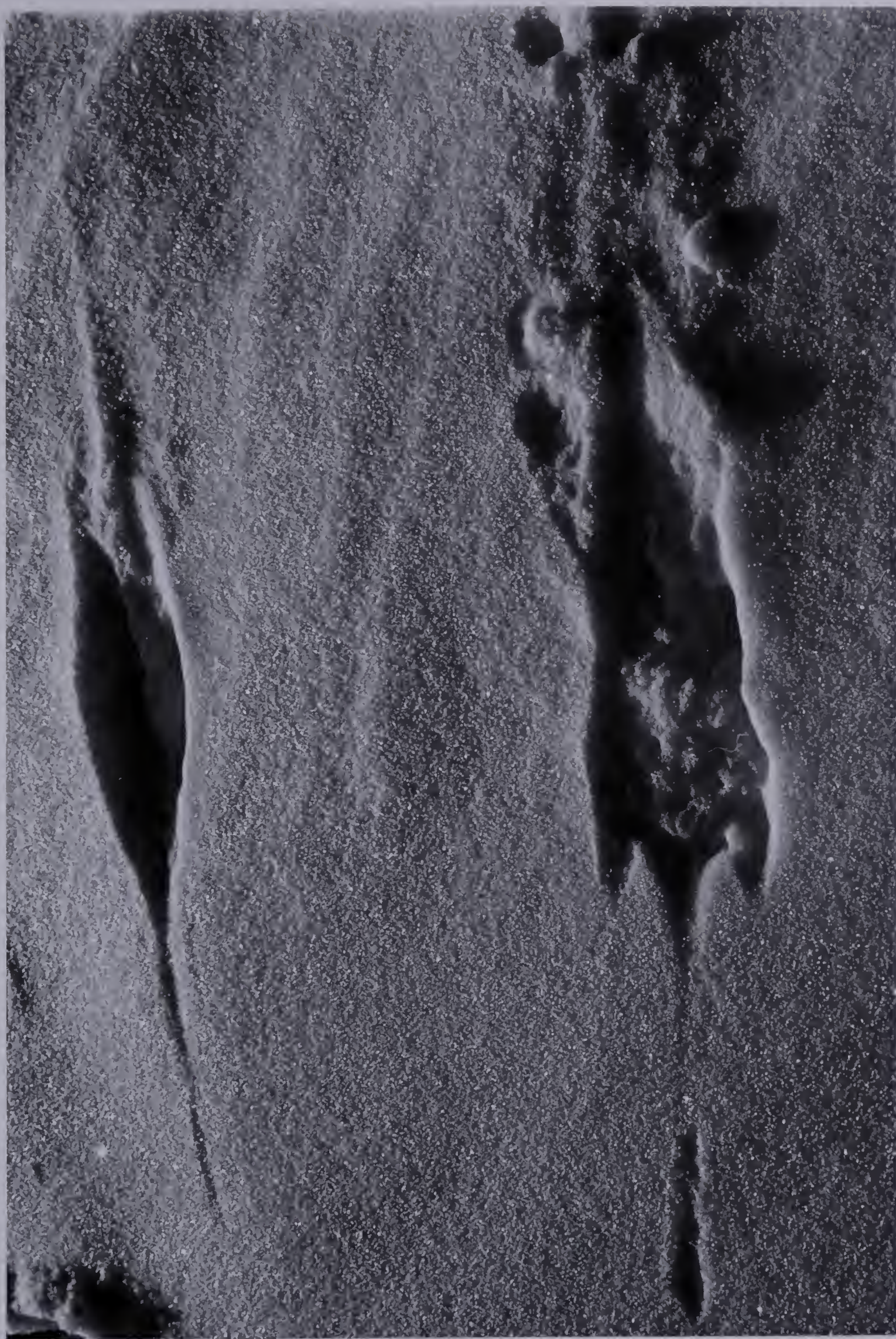




PLATE 73

"Sitzmark" and first stride.

This impression was made on March 15, 1965 after the squirrel had launched from the same point as in Plate 71. The heavily crusted snow below had been covered with a light new snowfall. The patagia have left impressions on either side. There was no over-reach in the first stride to the left as the hind feet were placed in the tracks left by the front ones. Subsequent strides were much longer, measuring 31, 29, 29 and 74.25 in respectively. X 0.42







### Braking

In general braking consists of manoeuvring the body into a position almost at right angles to the line of motion. This is clearly illustrated in Plates 64, 69, 70 and 74. Plate 69 illustrates the nearly horizontal braking attitude associated with parachuting while Plates 70 and 74 illustrate the more nearly vertical attitude associated with braking while gliding. In all cases the successive images clarify the general flight line. It should be noted that there is a marked tendency for the anterior end of the animal to be somewhat ahead of the right angles position and the posterior end somewhat behind. Also, the dorsal surface is arched convexly while the ventral surface tends to be somewhat concave. Thus air is deflected at higher velocity over the upper surface than the under, creating lift (Storer 1948). The retardatory effect of presenting the broad surface area of the squirrel to the air is clarified in Fig. 11 dealing with flying squirrel trajectories.

Plates 75, 76 and 77 illustrate that the collared turtle dove (Streptopelia risoria), the black-capped chickadee (Parus atricapillus) and the snowy owl (Nyctea scandiaca) appear to make use of the above principles when braking. In Plate 75, the black-capped chickadee is braking from an almost horizontal flight line. It has assumed an almost erect attitude braking with the broad surfaces of wings and tail. The snowy owl in Plate 76 is coming in at a sharper angle and



partially braking by maintaining the tail and inner portions of the wings at an angle almost perpendicular to the flight path. The dove in Plate 77 is maintaining a similar attitude while braking at an even sharper angle.

The morphology of the wings of birds and the flapping flight characteristic of most of the members of this group of vertebrates differs greatly from the patagia and gliding habits of flying squirrels. Naturally, there are profound differences in the aerodynamics of braking in the two groups.



PLATE 74

G. volans. Braking and Landing.

The successive stages in landing upon a vertical surface from a gliding phase are clearly illustrated. The somewhat horizontal attitude of the body assumes a more vertical position as the hind limbs are swung forward under the body, arching the spine. Fore limbs are moved into a position well forward as the head rotates backward. Note the paired action of both fore and hind limbs.

Subject at 4 ft.

Strobolume at 1200 cpm. High intensity



PLATE 75

Black-capped chickadee (Parus atricapillus) braking.

The chickadee is coming in for a landing along a flight path which deviates little from the horizontal. The body of the bird has assumed an approximately vertical position, virtually perpendicular to the line of flight.

Photograph at 1/5000 sec with Dormitzer Synctron electronic flash unit.





PLATE 76

Snowy owl (Nyctea scandiaca) braking.

The owl is approaching target at an angle of approximately  $45^{\circ}$  with the horizontal. This is an intermediate phase between those depicted in Plates 75 and 77. Again, the broad surfaces of wings and tail are approximately perpendicular to the flight line.

Photograph at 1/5000 sec with Dormitzer Syncron electronic flash unit.



PLATE 77

Collared turtle dove (Streptopelia risoria) braking.

The dove is braking at a sharp angle as it descends towards the perch below. The broad proximal surfaces of the wings and the broad surface of the tail present substantial areas across the line of flight.

Photograph at 1/5000 sec with Dormitzer Synctron electronic flash unit.







### Turning

Northern flying squirrels have a good deal of control over the direction of gliding and parachuting. Left turns, right turns, 180-degree turns, spirals and side-slips are all accomplished with dexterity. Slow motion photography (see accompanying film) clarifies the fact that the patagia tend to ripple a good deal when the squirrels are gliding. These ripples become more pronounced when the tension on the patagia is relaxed. The probable action of the tail as a stabilizer and rudder as well as the likely role of the patagia in controlling roll has been noted earlier (see page 157).

Relatively sharp turns appear to be the result of the combined effect of two basic shifts in body attitude. In the first place, the body rolls about its long axis and secondly, it yaws about the vertical axis. When these two motions occur simultaneously, the squirrel banks as a racing car does on a finely engineered curve. The roll seems to be initiated by the relaxation of tension on one of the patagia, depending upon the direction of the turn. This relaxation in at least some cases is brought about by either moving the fore limb on the appropriate side slightly posteriad or the hind limb anteriad (or both) or it may be accomplished by adducting the cartilaginous rod associated with the patagium. Yawing appears to be accomplished, in part at least, by swinging the tail sharply in the direction of the turn (Plate 78). This action provides drag in much the same manner as a paddle held in the water slightly to one



side of the stern of a moving canoe. The exaggerated rippling of the somewhat relaxed patagium on the inside of the turn might well provide significant additional drag.

In the single 180-degree turn which was observed in some detail, the squirrel was originally gliding almost due east in somewhat cramped quarters. It then suddenly swung from an approximately horizontal position into a steep vertical bank, reversed its direction, swung back again to the horizontal and then landed on the floor facing almost due west. The whole manoeuvre had been accomplished in a hallway 30 in wide while the distance from the initiation of the turn to its farthest extremity was in the neighborhood of 5 ft.

On several occasions wild flying squirrels were observed to side-slip in order to avoid the branches of trees in their path. The individual which habitually visited the bird feeding station performed this manoeuvre a number of times while gliding directly away into the bush from the power pole. On these occasions, there was no turning involved as the animal held to its straightaway course. While it was not possible to determine the mechanics involved, the manoeuvres were quite sharp. A side-slip to the right was sometimes followed almost immediately by one to the left, the whole experience leaving the observer with a profound respect for the aerial agility of these airborne acrobats. Speculation would suggest that perhaps a side-slip to the right is accomplished by relaxing the tension on the right





patagium while swinging the tail sufficiently to the left to counteract the drag developed by the exaggerated ripples in the relaxed patagium on the opposite side. But this is mere speculation and the actual execution of the manoeuvre may be much more subtle.

During the study period, wild flying squirrels were occasionally observed spiralling downwards around trees after having launched themselves from the topmost branches. Again, the details were not clear except that the squirrels were in the banking attitude with dorsal surface tilted inward. It could well be that this manoeuvre is accomplished largely in the manner of human skydivers who are able to rotate at will by merely raising or lowering a single limb (Sellick 1960). However, the slight accompanying roll of the body about its long axis suggests partial relaxation of the tension of the inner patagium in addition.

PLATE 78

G. sabrinus initiating a right turn.

The tension upon the right patagium is relaxed while the tail is flipped to the right and held there. The right side of the squirrel falls away and at the same time the animal begins to yaw to the right, resulting in a banking turn in the same direction.







### Airflow

Only a very limited amount of work was done in connection with airflow as it was practically impossible to persuade the animals to tolerate threads fastened lightly to the pelage. Nor was there a wind tunnel available for checking airflow over the surfaces of living organisms.

However, Plate 79 yields a little information about airflow over the upper surface during gliding and braking. In the upper image, the airflow is distinctly laminar as indicated by the attitude of the four-inch threads attached to the dorsal surface; the animal is at this point essentially in gliding position. In the next image the body has been brought into a position slightly more perpendicular to the flight line and the limbs have begun to swing downwards. Turbulence is just beginning to develop on the dorsal surface. In the next image, the angle of attack is still sharper. The back is arched and the former laminar airflow is breaking away from the dorsal surface. The stalling angle has been reached (Piercy 1945). In the final image, the animal has just landed. Turbulence both in pelage and threads is marked; the eddies are chaotic and all semblance of pattern is lost.

Savile (1962) notes that under some conditions it is possible to achieve laminar flow in aerial forms. Here, a layer of gas molecules is held against the wing and successive layers slide smoothly



over them like the cards of a deck being swept across a table. Usually the first requirement for laminar flow is a very smooth surface - at least as smooth as writing paper. It appears that the exceedingly soft, silky pelage, characteristic of all the gliders examined in the British Museum, might well serve these roles.



PLATE 79

Airflow in G. sabrinus.

While the squirrel is in gliding attitude as in the upper image, the airflow over the dorsal surface is essentially laminar. In the next image the animal has begun to assume landing attitude and the air stream begins to break away. Turbulence is still more pronounced in the second to last image while on landing, the eddies become chaotic.

Subject at 4 ft.

Strobolume at 1200 cpm. High intensity.





## IX. DISCUSSION

### Possible Selective Advantages of Gliding and Some Thoughts on the Evolution of Mammalian Gliders

It appears that gliding has evolved in the Mammalia in at least three separate lines, possibly four. There is little doubt that the Phalangerinae, Dermoptera and Petauristinae are distinct groups. The case for the Anomaluroidea is not so clear.

The three genera, Petaurus, Acrobates and Schoinobates of the Phalangerinae in the Order Marsupialia found currently in Australia and New Guinea are presumably related. Gregory (1961) states that the phalangeridae may be traced back to the Pliocene. In the Order Dermoptera, Simpson (1945) affirms the probable relationship between the two extant species of the genus Cynocephalus of Asia and the extinct genera Planetetherium and Plagiomene (Upper Paleocene and Lower Eocene) of North America. Young (1962) states that the Paleocene form shows that this line has been separate for more than 50 million years. The 12 genera which Simpson (1945) places in the subfamily Petauristinae of the family Sciuridae appear to represent yet another group in which the gliding habit has evolved independently. These flying squirrels of the northern hemisphere occur in Eurasia and North America from wooded areas in the Arctic, south to Indian and Ceylon, Java and Borneo and some southern Phillipines, and to discontinuous areas in Mexico, Guatemala and Honduras. Their





fossil forms are unknown before the Pleistocene of North America (Darlington, 1957).

In the family Anomaluridae, Simpson (1945) lists the genera Anomalurus and Idiurus under the subfamilies Anomalurinae and Zenkerellinae respectively. As noted earlier (pages 11-23) these forms differ in several respects from other gliding mammals. Darlington (1957) states that the relationships of this family are doubtful and that fossils often assigned to it are doubtful. Family Pseudosciuridae may belong here; it agrees in the attachment of the masseter. The cheek teeth are cusped or crested, with low crowns, while the skull is long and flattened. The several genera are found in the Eocene and Oligocene of Europe (Hill, 1961). They may also be related to the Theridomyidae of Europe (Upper Eocene to Middle Oligocene) and nine doubtfully assigned genera from Africa and Asia from the Upper Oligocene and Lower Miocene (Darlington, 1957). Despite the obscurity of the relationships of the Anomaluridae, Gregory (1961) contends that gliding has been acquired independently in all four of these groups.

Since there is so much evidence for the independent evolution of gliding behavior in mammals and since gliding forms are so numerous and widespread, one can conclude that the selective advantage conferred by the acquisition of this type of locomotion must be substantial. The problem would seem to resolve itself into an analysis of the probable advantages which would accrue to mammals which developed the



gliding habit, taking into consideration the natural conditions under which these forms tend to survive, the ecological niches which they occupy successfully.

There are numerous references in the literature regarding the tendencies of gliding mammals towards a nocturnal and arboreal existence. Fleay (1954), writing of the squirrel glider (Petaurus norfolcensis), refers to the nocturnal habits of this species and notes that the other flying phalangers are also nocturnal. He also refers to their habits of foraging for food in trees. Sanderson (1955) states that flying phalangers sleep by day in hollow trees.

Wood (1927), writing of a captive member of the Dermoptera, reports that they are almost if not entirely nocturnal. His specimen slept for most of the day with head tucked under the body between the forelegs. Wharton (1950) notes that dermopterans spend almost their entire existence in trees of various types and reports that they retire at or shortly before dawn to hollow trees, where they hang head-up by their sharp claws to the inside surface. They leave their retreats at dusk or on dark days shortly before the light has gone. Sanderson (1955) also refers to the tree-dwelling habits of the members of this genus and to the fact that they are active at night. Wood notes that when his captive "flying lemur" was placed on the ground it appeared to be just as helpless as a bat in similar position, and not being able to assume an upright position could only progress by a succession of short flapping leaps towards the nearest upright





object which it would immediately climb. Apparently, this form has sacrificed other types of locomotion in the interests of gliding and climbing.

Durrell (1956) reports that members of the genus Idiurus of the family Anomaluridae are strictly nocturnal and that they live communally in the hollow cavities of large trees. Sanderson (1937) concurs with respect to the nocturnal habits of Idiurus but notes that one subspecies of Anomalurus (A. beecrofti argenteus) is at least partially diurnal. However, the same observer, writing in 1955, states that all of the gliding anomalurids are wholly arboreal and move about only at night.

There are many references to the nocturnal and arboreal habits of the Petauristinae. Mr. H.C. Smith, who lived in Burma from 1915 until 1935 and collected specimens for the British Museum, writes (pers. comm., 1965) that Petaurista alborufus candidulus was the commonest form encountered in his area and that they were only observed when planing at dusk from tree to tree. According to local Malayan trappers quoted in Liat (1965) Petinomys genibarbis malaccanus starts gliding immediately after dusk. They nest in cavities in trees, often high above the ground. Tweedie (1965) recounts observing giant Malayan flying squirrels, Petaurista petaurista, planing down from vegetation high on a cliff to trees at lower altitude. He states that they seldom stir before sunset and are active mainly at night. Dr. E. Jacobson (cited in Tweedie, 1965) records that in the Padang Highlands of Sumatra the giant flying squirrels "come at dusk". Ellerman (1961)



mentions a specimen of Petaurista petaurista cineraceous as having been "shot at dusk, feeding in a Banyan tree". The same writer also states that Hylopetes fimbriatus is nocturnal, often living in the roofs of houses. Sanderson (1955) concludes that the Petauristinae, with the possible exception of the great Indian taguans (Petaurista), are nocturnal and get about among the tree-tops by means of prodigious leaps. He reports, further, that taguans have been observed basking in the sun, on their backs with their patagia spread wide. The single exception that I have run across with respect to the preference of the Petauristinae for an arboreal existence is reported by Prater (cited in Ellerman, 1961). Prater states that flying squirrels inhabit the tropical and temperate forests from plains level to an altitude coinciding with the limits of the tree line, but that a single exception to this rule is the woolly flying squirrel (Eupetaurus cinereus) which is found...."even in the treeless parts of Hunza and Gilgit, among barren rocks and cliffs". Presumably, this species utilizes its patagia in gliding from point to point in the rugged terrain in which it lives.

It seems appropriate, therefore, to speculate upon the possible selective advantages conferred upon nocturnal arboreal mammals by evolving the capacity to glide. The first possible advantage which comes to mind is that gliding may function as a form of escape behavior. Bourliere (1956) contends that for those animals that practise gliding flight, this is hardly more than a secondary mode of locomotion, and





is used principally, though not exclusively, as a means of escape. Wharton (1950) writes that Cynocephalus volans of southeastern Mindanao prefers hollow trees on the sides of steep ravines, trees tall enough to give them sufficient altitude for an escape flight. Fleay (1954) notes that felids and owls comprise the chief predators of gliding marsupials in Australia. Beebe (1927) gives a graphic account of the manner in which a giant flying squirrel in northern India escaped from a marten by gliding to a distant tree. Durrell (1956) recounts the manner in which great numbers of Idiurus escaped capture by his native hunters by gliding to surrounding trees.

Certainly in North America, the habit of foraging for food at night in the tops of trees without the necessity of coming to ground in order to move from tree to tree, would greatly reduce exposure to such night-prowling predators as the lynx (Lynx canadensis), bobcat (Lynx rufus), cougar (Felis concolor), coyote (Canis latrans), fox (Vulpes fulva), wolf (Canis lupus), pine marten (Martes americana), fisher (Martes pennanti), wolverine (Gulo luscus), long-tailed weasel (Mustela frenata), short-tailed weasel (M. erminea), etc. Gliding may also be an advantage in escaping from North American owls, most of which are nocturnal or crepuscular. Soper (1964) lists various squirrels as important food items in the diets of all of the above mammalian carnivores. Murie (1944) lists ground squirrels as important items in the food of foxes and, at times, in the diet of wolves in Alaska. Murie examined a total of 662 scats of the red fox during



three summers from 1939 to 1941 inclusive and noted that 46.3% of the scats contained ground squirrel remains, while 12.89% of the food items found in 1174 wolf scats during a three-year period consisted of ground squirrel remains. Surely had flying squirrels been readily available, they would have been utilized.

An additional advantage conferred upon mammalian gliders by their distinctive mode of locomotion would seem to be associated with food procurement. My own long experience with the northern flying squirrel (Glaucomys sabrinus) would support the contention of Soper (1964) that the preferred habitat of this species consists of open mixed woods in which the trees are often separated by considerable distances, rather than the denser coniferous woods preferred by the red squirrel (Tamiasciurus hudsonicus). Associated with this habitat preference is the fact that the northern flying squirrel rarely stores food in any quantity and hence must forage regularly, and often widely, for it. Nor can there be much doubt that most of this foraging is done in trees.

Despite the fact that northern flying squirrels are often caught in traps baited for other mammals (Hall and Kelson, 1959), a given area may support a sizeable population of the species with little evidence of their presence. In the winter of 1963-64, six northern flying squirrels were live-trapped by the writer in a woodlot of approximately 30 acres by placing the traps on platforms secured to the trunks of trees at heights of about 6 ft from the ground. No





flying squirrel tracks were observed in 16 careful examinations of the woodlot during the trapping period. In addition, with the exception of the tracks left by the flying squirrels which came to our bird-feeding station during the winter of 1964-65, flying squirrel tracks were observed in the snow on only three other occasions during the five-year study period. Notwithstanding, the wooded area of 26 acres immediately surrounding the writer's dwelling supported a population of wild flying squirrels throughout this period.

Davis (pers. comm., 1961) reported that his trapping success with respect to northern flying squirrels improved markedly when he transferred his traps from the ground to the lower branches of trees. Seton (1928) states that spruce seeds probably constitute the main food of the northern flying squirrel in Manitoba. Cahalane (1947) states that the northern flying squirrel's staple food is nuts and seeds, especially of hickory, beech, white oaks, pines and firs; but that mushrooms and other vegetation, insects, birds and eggs are consumed. McKeever (1960) reports the results of the examination of the stomach contents of 24 specimens of the northern flying squirrel in California during January to December, 1958. He found that during the winter hair moss was the principal food. Some fungi were consumed in the spring while in summer their entire diet consisted of fungi. Schmidt (1931) records a number of northern flying squirrels in Wisconsin visiting sapsucker holes in a birch tree in order to lick up the sap. The northern flying squirrels observed during my own study exhibited



a distinct partiality for such food items as pussy willows, buds of Populus tremuloides, Betula papyrifera and Salix spp., seeds of Picea glauca and the tender bark of young twigs of the above species with the exception of Picea glauca. They also consumed mosses, lichens and saskatoon berries (Amelanchier alnifolia).

Smith (pers. comm., 1965) writes that Petaurista alborufus candidulus was typically seen planing down from high up in a tree on one side of a jungle clearing to the bottom of a tree on the opposite side, presumably foraging for food. Ellerman (1961) reports the taking of a specimen of Petaurista petaurista cineraceous which was feeding in a banyan tree, and a specimen of Belomys pearsonii from a hole in a teak tree in a teak and bamboo forest.

Durrell (1954) notes that Idiurus kivuensis of the family Anomaluridae prefers more open woods and that the only food which the species could be persuaded to take in captivity consisted of palm nuts and avocados. Sanderson (1955) notes that in the wild, Idiurus appear to be insect-eaters rather than leaf-eaters.

Sanderson reports that the diet of flying phalangers of the genus Petaurus consists of insects, leaves, honey, nectar which they lick from flowers, the petals of various flowers and congealed gum which they obtain from the trunks, limbs and twigs of trees. Fleay (1954) states that the bulk of the diet of the flying phalanger, Petaurus norfolcensis, consists of insects, nectar from the blossoms of trees, sap from branches that have been pierced or stripped of bark





by their sharp teeth, sweet exudations from trees and the sugary substances of berries and fruits. He notes further that these gliders may have to travel considerable distances in order to procure their food.

According to Wharton (1950), wild flying lemurs (Dermoptera) tend to visit certain food trees regularly when their buds or fruits are in season. They feed upon various products of trees: the young seeds of Ceiba pentandra, the fruit of Ficus adamii, the leaves of Dracontomelum dao, Trema orientalis, Koordersiodendron pinnatum and Ficus adamii. From the study of a caged specimen, Wharton postulated that flying lemurs probably drink in the wild by licking wet leaves. Sanderson (1955) states that the Dermoptera have a leaf, fruit and flower diet. Wood (1927) also mentions the frugivorous diet of the Dermoptera. Liat (1965) states that Petinomys genibarbis malaccanus, in Malaya, feeds upon the ripened fruit of the durian tree.

It is clear that many of these gliding forms utilize trees for nesting, escape retreats, points of vantage from which to gain sudden momentum, and sources of food. Considering the conditions and circumstances associated with these activities, the evolution of their distinctive mode of locomotion would appear advantageous. It seems reasonable to hypothesize that by gliding, these forms are able to procure their varied necessities of life more efficiently as well as avoid many of the dangers to which they might otherwise be exposed.

Gliding and parachuting in the vertebrates, particularly in



the mammals, does not appear to be an "all or none" phenomenon. It has been demonstrated that while certain species are known to practise this mode of locomotion, related or morphologically similar forms may fail to assume a stable aerial attitude and hence, neither parachute nor glide (Oliver, 1951 and Cott, 1926). However, red squirrels (Tamiasciurus hudsonicus) when jumping from one branch to another at some distance or when shaken from a high tree, will spread their limbs and tail, assuming a relatively stable attitude, and land right way up. When falling from a considerable height their course is deflected much as that of a human sky diver. While red squirrels have probably never been considered as gliders, they do possess the sensory and nervous systems necessary for potential gliders or parachuters. It only remains for such forms to develop functional patagia. Apparently the initial step in becoming a glider is behavioral, through the development of attitude control, rather than structural (Savile, 1962).

Among the gliding mammals themselves, there probably exist various degrees of efficiency in this mode of locomotion just as there are variations in patagium development. The members of the genus Acrobates possess very narrow patagia indeed but, considering their small size, probably depend a good deal upon the flattened body and tail for gliding purposes. In none of the flying phalangers does there appear to be any accessory support for the patagia. In the Petauristinae the patagia are more highly developed and these forms have evolved a sizeable supporting cartilaginous rod projecting from the wrist and





activated by opposing musculature. Some of these forms are capable of sustained glides of up to a quarter of a mile in distance (Tweedie, 1965). In the Anomalurinae, the patagia are still more highly developed and often embrace the basal portion of the tail in a well-defined uropatagium. Additional support for these membranes is provided by a prominent cartilaginous rod projecting from the olecranon process. In the Dermoptera, we see the most highly developed patagia excluding those of the Chiroptera. Here, not only is the tail completely involved in the development of the interfemoral patagium, but also the digits in the interdigital patagia which, though pronounced, are not nearly so extensive as in the Chiroptera.

While relatively subtle yet highly significant functional skeletal modifications have undoubtedly occurred in the Phalangerinae, Anomaluridae and Petauristinae, outwardly these species do not appear to have deviated markedly from non-gliding forms and none appear to have sacrificed other modes of locomotion to any great extent in the interests of gliding and parachuting. It is true that there is some evidence that some species of the Anomalurinae are not quite as adept at climbing vertical tree-trunks as most other arboreal mammals. Sanderson (1937) describes the manner in which Anomalurus fraseri nigrensis accomplishes this feat: "...employing the two front feet together, then pulling up the two hind feet and arching the back like a giant loop-caterpillar. The backwardly-directed scales at the base of the tail are dug into the bark at the same time as the forwardly-directed claws on the hind feet, thus forming a rigid tripod



to support the animal while the fore feet are released and moved upward." However, the species is able to ascend a tree quite rapidly nevertheless.

The situation is quite different, however, with the Dermoptera. Skeletal modifications have occurred and the representatives are clumsy and relatively helpless on the ground (Wood, 1927). Here, as in the Chiroptera, specific modes of locomotion have been sacrificed in the interests of another type.

All of the gliding mammals with the exception of the Dermoptera have well-developed tails. Smith (1952) states that in practice the most important type of stability is that for rotation about the pitching axis and that in both gliding and flapping flight, stability in pitch can be ensured by the presence of an adequate horizontal surface behind the centre of gravity. It may well be that the interfemoral patagium of the Dermoptera serves this purpose, or perhaps this form has exchanged a measure of stability for instability and manoeuvrability as in the bat. It does not appear improbable that all true fliers evolved through a gliding stage. Certainly Archaeopteryx possessed such a long flat tail with feathers springing pinnately from its margin. Rhamphorhynchus also possessed a long tail with terminal fluke, which could have served as a stabilizer.

Whether efficiency in gliding actually increases with patagium development from Acrobates through the Petauristinae and Anomaluridae to the Dermoptera remains to be demonstrated. Sanderson (1955) reports





that members of the Dermoptera glide from tree to tree in the forest sometimes covering as much as 100 ft between them, losing only about one part in five in altitude. Smith (pers. comm., 1965) writes that Petaurista alborufus candidulus glides at about an angle of  $45^{\circ}$ . Liat (1965) states that his captive specimen of Petinomys genibarbis malaccanus glided for limited distances at an angle of about  $53^{\circ}$ . Durrell (1956) reports that he saw an individual Idiurus leave the trunk of a tree at a height of about 30 ft, glide across a dell in a steady swoop and land on a tree about 150 ft away, losing little, if any, height in the process. Sanderson (1937), writing of Idiurus macrotis, notes that when he disturbed a number of them in the daytime he observed them "...take to the air in clouds, floating away among the neighbouring trees like bits of soot from a chimney, steering themselves over and around obstacles with the facility of birds, and landing silently, hundreds of feet away, without any apparent loss of height."

It is difficult to assess the subjectivity of the above statements and the conditions under which the subjects were performing. My own records of Glaucomys sabrinus show that they tend to lose about 1 ft in 3 during sustained glides.

It is important to realize that there does not appear to be any necessity for the evolution of the capacity for sustained gliding to occur at a single step. Rather, any slight modification in this direction might prove distinctly advantageous to the form concerned.



The capacity to maintain a stable aerial attitude so as to land uninjured after falling from a height would appear to have important survival value for an arboreal form. The addition of structural modifications would most certainly render this mode of descent more efficient.

There is great need for further objective studies of all modes of locomotion practised by the various groups of gliding mammals in order to elucidate subtle similarities and differences in morphology and function.





## SUMMARY

Some aspects of the locomotion and associated morphology of the northern flying squirrel, Glaucomys sabrinus, were investigated during the years 1960 to 1965 inclusive. A limited amount of study of the southern flying squirrel, G. volans, and of the red squirrel, T. hudsonicus, was done during the final year for purposes of comparison. The morphological work involved investigation of growth rates, body and skin densities, areas of specific surfaces, and the extent and activation of the cartilaginous rod which partially supports the patagium. The locomotor activities studied involved progression upon horizontal and vertical surfaces, as well as progression through the air. The latter included analyses of trajectory, gliding, parachuting, launching, landing, braking, turning and a minimal investigation of airflow. Much of the work was done by the use of single and multiple image high-speed still photography as well as by slow motion cinematography.

In general, growth rates were not unlike those recorded for other mammals. Birth was followed by a period of rapid growth which tapered off gradually. Hind foot and ear attained near-maximum length sooner (50 days) than tail and total body (56 and 60 days respectively), while body weight tended to continue to increase gradually for approximately a year. The young were naked, blind and unpigmented at birth with the ears folded and fused to the head. Pigmentation and pelage appeared first on the dorsal regions except



for the chin which exhibited fine short white hairs on the first day after birth. The pinna had unfolded completely by day 6, while the lower incisors, although still beneath a thin transparent membrane, were 3 mm in length by day 18. A single individual had its eyes open by day 29, while the upper incisors appeared on day 33.

Early attempts at locomotion occurred on the first day as the young attempted to squirm forward on the belly while moving the limbs in a rather uncoordinated fashion. By day 4 they were able to turn over when placed on their back and could turn in circles about the pelvis using the front limbs for propulsion. By day 6 the young were able to cling to the fingers when handled and could support the head in an upright position. On day 12 they were observed progressing backwards by pushing with the fore limbs, and exhibited the spreading reflex when suspended by the tail. By day 40 the young were able to ascend vertical surfaces slowly, but were unable to descend. On day 49 they were able to prop themselves on their haunches, freeing the fore limbs for food handling. Hind limbs remained relatively weak until about day 50. By day 58 they were able to make 8-inch horizontal jumps following much head bobbing. By this time they were also able to descend tree trunks. By day 66 the young were making leaps of 2 - 3 ft, spreading the patagia fully, while by day 70 they were able to glide for distances up to 6 ft.

The total density of intact northern flying squirrels was found to be significantly lower than that of red squirrels. The





densities of the skinned bodies and of the skins of the two species were not significantly different. However the patagia of northern flying squirrels increase the ventral surface area by approximately 77% and hence the increase in amount of cutaneous tissue and pelage appears responsible for the difference in total density.

The patagium is partially controlled by a cartilaginous rod approximately 28.5 mm in length, attached laterally to the pisiform bone. This rod is adducted and abducted by opposing musculature.

Northern flying squirrels were observed walking when crawling as juveniles, when foraging casually for food upon the ground, or when slowly descending tree-trunks. In the adults support often alternated between two, three and four feet, while in juveniles the support pattern involved three and four feet successively.

Trotting was observed only when the squirrels were progressing along slender branches and occurred both when the animals were right side up and when they were upside down. Occasionally the trot was briefly transitional between the walk and bound.

Most of the observed progression of northern flying squirrels upon horizontal surfaces was by means of the bound or half-bound. These gaits were characterized by conspicuous arching of the spine associated with the over-reach of the hind limbs. Two periods of suspension were observed, a relatively long one during which the body was stretched out in mid-air, and a much shorter one when the front limbs left the running surface immediately prior to the contact of the



hind ones. Running rates of up to 6.1 m.p.h. were recorded for G. sabrinus, but strides were a good deal shorter than those made by wild individuals under natural conditions. The running rates for G. volans were slightly higher than those for sabrinus.

Both species of North American flying squirrels tended to lay scent trails when introduced to new surroundings.

Northern flying squirrels tend to ascend trees by means of a footfall pattern in which fore and hind limbs move in pairs. When descending they may either walk or use the front and hind feet in paired fashion.

Travel through the air is characterized by gliding and parachuting. Short trajectories are essentially parabolic but the patagia exert a retardatory effect upon the rate of descent. Launching is accomplished by the pull of the fore limbs and the powerful thrust of the hind limbs. Braking is associated with manoeuvring the broad ventral surface into a position approximately perpendicular to the line of flight. When landing upon horizontal surfaces the hind feet commonly make contact before the front feet, while the order is reversed when landing upon vertical surfaces. Northern flying squirrels can make relatively sharp 90-degree turns, spiral descents and even negotiate sudden changes of direction through  $180^{\circ}$  while in the air. Turning appears to be initiated by the lowering of a front limb and the relaxation of the tension on the patagium on the same side, together with flipping the tail in the direction of the turn. Airflow





appears to be laminar during gliding phases, but turbulence develops as the squirrel brakes for landing.

Gliding in the mammals appears to have evolved independently on at least three occasions, possibly four. Flying phalangers of the subfamily Phalangerinae (Order Marsupialia) are represented by the genera Petaurus, Acrobates and Schoinobates occurring in Australia, Tasmania, New Guinea, and various islands to the north. The Dermoptera is represented by a single genus, Cynocephalus, of Asia. Two African genera of gliding mammals, Anomalurus and Idiurus, are listed with the ?Sciuromorpha under the subfamilies Anomalurinae and Zenerellinae respectively. An additional twelve genera of gliding mammals are listed under the subfamily Petauristinae of the family Sciuridae. The latter occur in North America, Europe, Asia, Ceylon and the Indonesian islands. Study skins and skeletons housed in the British Museum reveal a great range in size and coloration as well as more subtle differences in morphology.

Gliding and parachuting also occur in various species of fish, amphibians and reptiles. A well-developed sense of balance and the ability to control aerial attitude appear to be basic to successful gliding.

PLATE 80

"On Camera," during coffee break.







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## APPENDIX A

Table      Mean growth rates of three specimens  
of Glaucomys sabrinus, born May 8, 1959.

Day	Weight (grams)	Total Length (mm.)	Tail (mm.)	Hind Foot (mm.)	Ear (mm.)	Cartilaginous Rod      Length (mm.)
1	.	.				5.0
2	6.9	74.1	24.0	6.0	4.0	
4	7.1	77.1	27.3	9.3	4.0	
6	8.6	81.7	27.7	9.7	6.0	7.3
8	9.8	87.3	31.0	10.7		8.3
10						9.5
11	13.2	101.3	36.7	12.0	6.5	
13	14.8	110.7	39.0	13.0	7.0	11.4
15	17.2	115.3	41.0	13.0	7.5	12.6
17	17.3	120.7	45.0	16.0	8.0	
19	23.9	128.3	49.0	17.3	9.0	
20						17.0
21	24.8	133.0	53.7	18.0	10.0	
24	27.8	145.0	56.0	20.0	11.0	20.3
26	31.0	151.0	60.3	22.7	11.0	
27						21.5
28	32.8	155.0	62.7	24.0	12.0	
30	34.1	160.0	64.3	25.0	15.0	
31						22.2
33	36.9	169.3	68.3	26.3	15.0	
35	40.1	176.7	74.3	28.0	15.0	
38	45.1	191.3	78.0	30.0	17.0	
40	47.6	196.3	80.3	30.3	18.0	24.1
42	47.3	199.0	81.7	31.3	18.0	
44	49.7	250.3	89.3	32.3	19.0	
46	55.0	216.3	93.0	34.0	20.0	
48	59.5	221.7	97.7	34.7	20.0	
50	63.2	232.3	104.7	35.3	21.0	24.7
56	70.8	257.3	121.7	36.7	21.5	
60	71.4	267.4	127.0	38.0	22.0	
63	76.3	276.2	130.0			
69	83.2	283.2	133.3	40.3		
73	87.3	289.4	137.7	40.3		
75	90.1	293.3	140.0	41.0		
79	93.3	297.5	143.0	41.7	23.5	
87	98.6	300.0	144.3	41.7		
93	102.2	301.5	144.7	41.7	24.0	26.1

(continued)





Table      Mean growth rates of three specimens  
of Glaucomys sabrinus, born May 8, 1959.

Day	Weight (grams)	Total Length (mm.)	Tail (mm.)	Hind Foot (mm.)	Ear (mm.)	Cartilaginous Rod      Length (mm.)
99	103.2					
120	110.5					
125	116.2					
129	125.2					
135	124.5					
142	127.8					
150	125.3					
156	123.1					
177	118.6					
184	126.6					
191	126.2					
198	132.5					
205	142.6					
212	143.4					
219	149.0					
226	152.5					
233	150.6					
240	148.2					
247	159.8					
254	165.9					
261	156.0					



## APPENDIX B

Notes to Accompany the Film, 'Locomotion of the Northern Flying Squirrel'.

The accompanying motion picture film clarifies a number of details and relationships not clearly demonstrated in the still photographs. The fumbling, relatively ineffectual attempts at locomotion in the young flying squirrels are succeeded by the graceful motions of the adults in which one phase of locomotor activity flows smoothly and rhythmically into the next. Hence, most of the following sequences contain several such integral phases.

The activities of the young squirrels were photographed at 24 frames per sec since their actions tend to occur much more slowly than those of the adults. Running, launching, landing, climbing, gliding and parachuting in the adult squirrels were all photographed at 128 frames per sec so that when projected at silent speed with the standard projector the viewer is able to observe these actions slowed down by a factor of 8, giving him a much better opportunity to analyze successive events. Even so, the succession of limb movements is often so rapid that details are not easily discerned.

In the nest at age one day.

The activity of young northern flying squirrels at this stage is characterized by alternating periods of intense physical exertion and periods of almost complete inactivity during which they lie motionless in the nest. The actions themselves appear rather uncoordinated as the squirrels push, pull, squirm and roll about in the nest. It





should be noted that they spend much of the time on either lateral or dorsal surface and that the mouth is often gaping. Such activity is undoubtedly associated with searching for the teats of the mother. The anterior end of the body appears relatively heavy and is often pushed ahead snowplow-fashion. The brief sequence shows at least two somewhat hesitant examples of the lateral walk in which one fore limb is advanced and followed by the hind limb on the opposite side which, in turn, is followed by the other front limb and its opposing hind member.

Age 8 days.

At this stage we again note the squirming lateral walk characteristic of the young squirrels. The limbs project laterally in salamander fashion as the squirrels advance slowly on their bellies. A single individual demonstrates the capacity to turn over when placed on its back, assisted by the rough surface of the towel-  
ing upon which it has been placed. The single squirrel advancing into the frame from the upper left-hand corner is utilizing a slow lateral walk in which the sequence of limb movements is right hind, right front, left front and left hind. Since only a single limb is advanced at a time, support alternates between three and four feet plus the constant support provided by the ventral surface of the animal.

Age 11 days.

Though now three days older, this squirrel is unable to right



itself when placed upon its back on a relatively smooth surface. However, it is able to raise the anterior portion of the body to some extent. When suspended by the tail the young squirrel exhibits the spreading reflex in which all the limbs are extended fully, the patagia stretching taut between wrist and ankle. At this age, this attitude tends to be maintained rather steadily with little movement on the part of the limbs. When lowered, the squirrel clings to the fingers with its fore limbs. At this stage, the hind limbs appear relatively weak.

Age 16-18 days.

One of the squirrels is able to turn over after considerable physical effort and immediately rests in a sprawling, relaxed fashion. Progression tends to be backward with most of the effort exerted by the fore limbs.

Age 18-26 days.

The squirrel tends to circle a good deal about the pelvis using the front limbs alternately for most of the propulsive effort. The hind limbs still project widely and most of the contact with the substrate is made with the heels rather than the plantar surfaces or digits. When progressing in a backward direction the front limbs are used either alternately or in paired fashion; the back is markedly arched in the lumbar-sacral region. The plagiopatagia are in broad contact with the substrate while the propatagia are clearly visible when the squirrel spreads its fore limbs. Periods of activity are





succeeded by periods of rest.

When clinging to a narrow log held at an angle of  $45^{\circ}$  from the horizontal the squirrel's body tends to be closely appressed to the surface with the fore limbs clasping it firmly and the digits and claws gripping the bark. Although the hind limbs are in contact with the log throughout much of their length, the hind feet appear unable to obtain a grip. The tail tends to wrap around the log. When the log is slowly raised to a vertical position, the squirrel continues to cling briefly before falling. In the following short sequence, the squirrel visibly "starts" at the sound of a hand-clap indicating that the external auditory meatus is now open and the ears functional.

When clinging to the underside of the same narrow log held horizontally, the squirrel clearly depends upon the fore limbs for the majority of the effort although the hind limbs are able to function to a limited extent as their plantar surfaces and claws grip the bark. When the log is slowly rotated the squirrel is able to struggle into a position on its upper surface.

Age 28-30 days.

The squirrel is now able to gather the hind limbs under the body. The patagia are somewhat retracted indicating the development of the associated musculature. Progression still tends to be either in a backward or circular direction. Limb movements are much more rapid but the diagonal walk is often utilized. When exhibiting the spreading reflex, the dorsal surface tends to be much more concave than at age 11



days. Also the limbs tend to be much more active, moving forward and backward in zig-zag fashion reminiscent of the motion of the limbs of the adults during early gliding and parachuting phases. The cartilaginous rod at the wrist does not appear to come into play at this age. The fore and hind limbs tend to be used alternately rather than paired as in most of the running gaits of the adults.

#### Running.

As the squirrel bounds along the log, two periods of suspension are noted; a relatively long one during which the animal is stretched out in mid-air, and a relatively short one when the front feet leave the running surface just prior to the contact of the hind ones. The leap to the vertical log tends to be preceded by shortening of the stride.

In the ascent of the vertical log, the front and hind limbs move in paired fashion but the front members are more spread than the hind ones. During the brief glide the patagia are spread but since the glide is a short one, the hind limbs are quickly swung forward and under the body so that landing occurs from a vertical position with all four feet striking nearly simultaneously. In the descent of the log, while the fore and hind limbs are usually used in pairs, occasionally the diagonal walk is utilized. The entire plantar surfaces of the hind feet grip the log securely. The hind feet are broadly spread while the front feet move well under the body, in marked contrast with the ascending attitude. During the descent the squirrels often pause





with the head directed outward and one hind foot extended well to the rear. When landing upon the floor, the hind limbs are swung well forward under the body prior to contact so that they take the major shock of landing.

When running along a narrow log, the bound is utilized and the tail clearly functions as a balancer. The squirrel often lands on the far side of the log where it is shielded from the direct glare of the flood lights.

#### Launching.

While many launching sequences have been shown earlier in connection with very short flights, the following series clarify a number of details associated with somewhat longer glides. When launching from the margin of a horizontal surface the squirrel advances and grasps the edge of the surface with its fore feet and then works the hind feet well forward under the body. The body is then drawn backward as far as possible, cocking the musculature and conferring maximum purchase for the effort of take-off. Launching is accomplished by the pull of the fore limbs and the powerful thrust of the hind members. In the running take-off of one individual, no shortening of stride is apparent before launching. A short sequence shows the smaller North American species, G. volans, launching from a head-downward position.



### Landing.

The limbs absorb the major shock of landing as they are extended well forward of the body prior to contact. It should be noted that here the extended limbs "give" with the forward motion, absorbing the shock and allowing the ventral surface of the animal to flatten gradually against the landing surface. At the conclusion of longer glides, the front limbs tend to contact the vertical surface first.

### Gliding and Parachuting.

During early gliding phases there is a good deal of adjustment of the limbs and patagia until stable gliding attitude is attained, although these adjustments are not apparent to the naked eye when they are occurring at normal tempo. It would appear that these adjustments are also associated with setting course. Once stable gliding attitude is attained, the squirrel glides smoothly downward towards the target, with only minor rippling of the patagia.





### Frame by Frame Analysis

Frame by frame analyses of a limited number of bounding sequences gave running rates varying from 6.1 to 9.9 mph. Stride intervals varied from 0.13 to 0.16 sec. In general, as rate of speed increased, length of stride tended to increase from a minimum of 14 in to a maximum of 28.2 in while rate of stride tended to decrease. As velocity increased, the length of unsupported periods varied from 23.5 to 70% of the stride interval. As speed decreased, there tended to be less and less over-reach of the hind limbs and the second unsupported period of the stride tended to disappear.



## APPENDIX C

### Trapping, Housing and Maintenance of Northern Flying Squirrels.

There are at least two successful methods of securing live northern flying squirrels for study and experimental work. Before proceeding with such attempts however, it is important to survey the trapping area carefully. The wooded region ought to be rather open with a mixture of conifers and deciduous species and containing numbers of trees with woodpecker excavations which might serve as nesting sites for flying squirrels. The species appears to be particularly fond of wooded ravines containing at least a trickle of water. Live traps should be placed upon platforms or branches, close to the trunks of trees and at least 5 or 6 ft from the ground. Sunflower seeds, peanut butter or a mixture of bacon grease and rolled oats are satisfactory baits. Specimens may also be secured during the daytime by using a strong nylon butterfly net wired to a long slender pole. In this case, the hoop of the net is held closely pressed to the tree and encircling the entrance to the nest while the trunk of the tree is thumped vigorously with a stout stick.

Once secured, the squirrels should be housed in outdoor cages measuring at least 4' X 8' by 6' high. One-quarter-inch mink wire is suitable for covering the sides and bottom of the cage while a piece of 8' X 4' plywood makes an excellent roof if sloped for purposes of drainage. Nesting boxes may be constructed of boards or sections of stumps containing woodpecker cavities and are best placed





upon a platform 3 or 4 ft from the ground. It is important to supply quantities of nesting material such as bits of wool, terylene animal bedding, feathers, fine grass and branches of willow with shaggy bark which may be shredded by the squirrels.

It is important that the squirrels have an adequate supply of fresh clean water which may be dispensed by the use of drip bottles or inverted water jars as provided for poultry chicks. The species does well on such food items as sunflower seeds, rolled oats, nuts, berries, apples, pussy willows, buds of Aspen tremuloides, Betula papyrifera, Salix spp., spruce cones, lichens and fungi of various kinds, rose hips, grapes, tomatoes, oranges and the bark of young twigs, especially Aspen tremuloides and Salix spp. Undiluted evaporated milk seems particularly important during the nursing period.

Four or five pairs of flying squirrels will share a cage of the above dimensions and it is not necessary to separate the sexes when the young are being reared if a sufficient number of extra nesting boxes are provided during this period. If reproductive success is desired, it is essential that the adult squirrels be disturbed as little as possible during late April, May and June when the litters are arriving.







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